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Frugivory-related traits promote speciation of tropical palms

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Animal-mediated seed dispersal by frugivorous birds and mammals is central to the ecology and functioning of ecosystems, but whether and how frugivory-related traits have affected plant speciation remains little explored. Fruit size is directly linked to plant dispersal capacity and therefore influences gene flow and genetic divergence of plant populations. Using a global species-level phylogeny with comprehensive data on fruit sizes and plant species distributions, we test whether fruit size has affected speciation rates of palms (Arecaceae), a plant family characteristic of tropical rainforests. Globally, the results reveal that palms with small fruit sizes have increased speciation rates compared with those with large (megafaunal) fruits. Speciation of small-fruited palms is particularly high in the understory of tropical rainforests in the New World, and on islands in the Old World. This suggests that frugivory-related traits in combination with geography and the movement behaviour of frugivores can influence the speciation of fleshy-fruited plants.

The dispersal of seeds by fruit-eating animals such as birds and mammals is a key plant–animal interaction, especially in the tropics[1,2]. Frugivores constantly move around the seeds of animal-dispersed plants and thereby affect dispersal, gene flow and genetic structure of plant populations[3]. This ultimately can influence plant speciation[2]. Of particular importance for speciation are the frequencies of both restricted and long-distance dispersal because the degree of genetic divergence of plant populations depends on them[2,4]. To date, few case studies have examined the relationship between seed dispersal and speciation in animal-dispersed plants[2,4], and large-scale studies testing the generality of this relationship remain scarce[5].

Fruit size is a key trait in plant–frugivore interactions (Table 1). Fruit size sets a limit to the ingestion of fruits by relatively small-sized seed dispersers and therefore tends to be positively correlated with body sizes and gape widths of consumers[6,7]. Large fruits such as megafaunal fruits (>4 cm in size[8,9]) are predominantly dispersed by large-bodied, non-flying mammalian frugivores (for example, elephants, a number of extinct proboscideans, tapirs, large primates, ground sloths) that have large home ranges[10,11]. This leads to frequent dispersal across large distances, high gene flow among plant populations and a low speciation probability[2]. In contrast, small fruits are predominantly dispersed by small- and medium-sized frugivores, including frugivorous birds, bats, scatter-hoarding rodents or other small-bodied non-flying mammals, and fish. Compared with mammalian megafauna, these frugivores generally have smaller home ranges and less frequent dispersal across large distances[2], and island colonization is possible (for example, via birds and bats)[12]. The more 'restricted dispersal' of non-megafaunal frugivores combined with occasional long-distance dispersal, as typically suggested from fat-tailed seed dispersal kernels[3], can promote the divergence of isolated plant populations and hence increase the probability of speciation[2]. Consequently, a higher speciation rate can be predicted for plant lineages with small fruits compared with those with large, megafaunal fruits ('fruit size hypothesis', H1 in Table 1).

Beyond fruit size, plants with animal-dispersed fruits in the understory of tropical rainforests have been associated with high speciation rates[4], especially when compared with taller plant growth forms (for example, canopy trees) (Table 1). This could be caused by the sedentary nature of small- and medium-sized seed dispersers in the forest understory because their spatially restricted dispersal will result in low gene flow among plant populations[13,14] and thus a higher probability of allopatric plant speciation[4]. Animal-dispersed understory plants should therefore diversify more extensively than other plants[4], especially in regions where small-bodied understory birds are abundant and species rich[15]. This predicts a higher speciation rate of understory lineages compared with other growth forms ('understory habitat hypothesis', H2 in Table 1). Only a few studies have tested the understory habitat hypothesis[4,16] and it remains unclear how general and widely applicable it is across taxa and regions.

Oceanic barriers make seed dispersal to islands challenging. The isolation of islands can restrict colonization and limit gene flow among plant populations (Table 1). Long-distance dispersal of animal-dispersed plants to remote oceanic islands is facilitated by frugivores that are strong fliers and hence able to cross large stretches of open water, including birds such as hornbills, macaws and fruit pigeons, and volant mammals such as fruit bats[12,17]. Seed dispersal to remote islands is therefore generally rare, leading to increased possibilities for genetic differentiation by isolation and allopatric plant speciation ('island colonization hypothesis', H3 in Table 1). Especially on islands that have been isolated for millions of years (that is, volcanic islands or atolls), plant speciation rates can be expected to be higher compared with the mainland or continental islands because the latter have experienced more connectivity (and hence gene flow) through geological time. Although adaptive radiations

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Table 1 | Key hypotheses of how frugivorous vertebrates influence plant speciation

Hypotheses	Explanation	Case studies and lines of evidence	References
H1: Fruit size			
Speciation of plants with small fruits is higher than speciation of large, megafaunal-fruited plants	Dispersal of large-fruited plants by large-bodied frugivores leads to high gene flow among plant populations and therefore reduces the probability of genetic differentiation and allopatric speciation[2]	1. Fruit size of vertebrate-dispersed plants correlates with body size (or gape width) of their frugivorous consumers so that large-fruited plants are dispersed by large-bodied frugivores	7
		2. Large-bodied birds and mammals have larger home ranges and movement distances than small-bodied species	10,11
		3. Fruit sizes of species in trans-regional plant genera are smaller in regions where large-bodied mammalian frugivores have been absent (for example, New Zealand) compared with regions where plants have evolved in the presence of such frugivores (for example, Australia)	6
		4. Fruit sizes of vertebrate-dispersed plants become smaller at sites where large-bodied frugivores have become functionally extinct	29
H2: Understory habitat			
Plants with small, vertebrate-dispersed fruits in the understory of tropical moist and wet forests have higher speciation rates than taller plants	Vertebrate-dispersed understory plants have low gene flow among populations because dispersal distance by sedentary understory frugivores is spatially restricted. This increases the probability of genetic differentiation and allopatric speciation[4]	1. Avian seed dispersers in the understory show spatially restricted dispersal and therefore higher genetic divergence and more subspecies than canopy birds	13,14
		2. Several vertebrate-dispersed plant genera in tropical forest understories show an extraordinary species richness	4
		3. Clades of Neotropical vertebrate-dispersed understory plants are more species rich than understory sister clades with dry fruits	16
H3: Island colonization			
Vertebrate-dispersed plants on oceanic islands have higher speciation rates than plants on the mainland or on continental islands	Oceanic barriers lead to restricted colonization and limited gene flow among plant populations, which increases the probability of genetic differentiation and allopatric speciation[4]	1. Avian seed dispersers show higher speciation rates on oceanic island archipelagos than on the mainland, possibly because limited dispersal leads to high genetic differentiation	38
		2. Rapid radiations of plants have been described for oceanic island archipelagos as well as island-like mountainous habitats	18,39
		3. Long-distance dispersal of vertebrate-dispersed plants to oceanic islands or fragmented habitat patches is dependent on occasional movement of large-bodied volant frugivores (for example, hornbills, fruit pigeons and fruit bats)	12,17

on islands have been studied extensively[18], tests of the island colonization hypothesis for animal-dispersed plant taxa remain sparse.

Here, we quantify speciation rates in relation to fruit size, understory habitat and island colonization in palms (Arecaceae), a species-rich animal-dispersed plant family typical for tropical rainforests[19,20]. Among angiosperm families, the palm family is one of the major food plant groups for vertebrate frugivores in the tropics[2] and a large number of both avian and mammalian frugivores have been observed to feed on them[21]. Together with data on fruit sizes, growth forms and species distributions, we estimate speciation rates from a species-level phylogeny of the palm family[22] globally as well as separately for the New World (including South, Central and North America and the Caribbean) and the Old World (including Australia, Indomalaya, Oceania, Pacific, Africa, Madagascar and surrounding islands)[23]. More specifically, we tested the following three hypotheses (Table 1): (H1) palms with small fruit sizes (<4 cm) have higher speciation rates than palms with large fruit sizes (that is, megafaunal fruits ≥4 cm); (H2) understory palms (especially those with small fruits) show higher speciation rates than canopy palms; and (H3) dispersal to oceanic islands has increased speciation rates compared with speciation on the mainland and continental islands.

Results

The majority of palms have relatively small fruits (<4 cm in length; $n = 1{,}607$ species), but about 12% of all sampled palm species ($n = 229$) have large, megafaunal fruits, defined as being ≥4 cm in length[8] (Fig. 1). Overall, fruit sizes of animal-dispersed palms vary widely from small 0.4–0.5 cm fruits in some *Areca*, *Bactris*, *Calamus*,

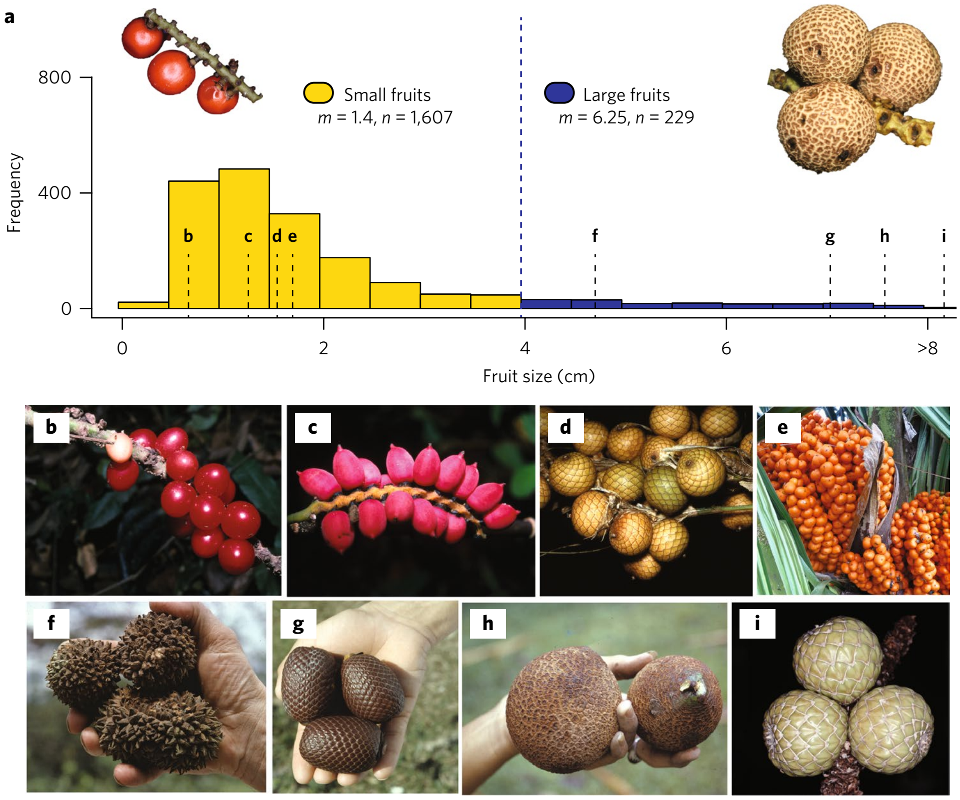

Fig. 1 | Global variation in palm fruit size. **a**, Fruit sizes of all species in the analysis ($n = 1{,}836$ extant palm species). The classification of small (<4 cm) and large, megafaunal fruits (≥ 4 cm) as used in the models in this study is indicated, as well as the median (m) and sample size (n) for each of these groups. Small fruits: *Licuala parviflora*; large fruits: *Lemurophoenix halleuxii*. **b**–**i**, Pictures illustrating the diversity of vertebrate-dispersed fruits in palms, representing small-fruited (**b**–**e**) and large, megafaunal-fruited (**f**–**i**) palms. **b**, *Iguanura elegans*. **c**, *Pinanga disticha*. **d**, *Calamus erioacanthus*. **e**, *Ravenea dransfieldii*. **f**, *Manicaria saccifera*. **g**, *Mauritia flexuosa*. **h**, *Pholidocarpus sumatranus*. **i**, *Metroxylon sagu*. Credits: **a**, small fruits, Anders Barfod; large fruits, John Dransfield; **b**–**f**,**h**, John Dransfield; **g**, Andrew J. Henderson; **i**, William J. Baker.

Chamaedorea, *Coccothrinax*, *Dypsis*, *Geonoma*, *Licuala* and *Pinanga* species to large >10 cm fruits in genera such as *Borassus*, *Metroxylon* and *Phytelephas* (Supplementary Table 1). Some palm species with particularly large fruits such as the coconut (*Cocos nucifera*, 22.5 cm fruit size), the nipa palm (*Nypa fruticans*, 11.5 cm fruit size) and the double coconut (*Lodoicea maldivica*, 45 cm fruit size) are not dispersed by animals (Supplementary Table 1). Apart from these few exceptions, all other palm species have vertebrate-dispersed fruit types (drupes and berries) and both birds and mammals are their main seed dispersers[21].

Fruit size-dependent speciation. Using information on fruit sizes of 1,836 palm species together with the Binary State Speciation and Extinction (BiSSE) model[24] we tested whether small fruits are associated with high speciation rates (H1, Table 1). The best fitting BiSSE model showed that speciation rates of small-fruited palm lineages are higher than those of large, megafaunal-fruited palm lineages (H1; Fig. 2). This supported the fruit size hypothesis both globally (Fig. 2a) and in the Old World (Fig. 2c), but interestingly not in the New World (Fig. 2b). A potential confounding factor between speciation rate and fruit size could be the allometric relationship between fruit size and overall plant size because plant size might be a proxy for generation time (Supplementary Fig. 1). Using data on palm stem heights as a measure of overall plant size showed that the high speciation rate of small-fruited palm lineages persisted when overall plant size was accounted for (for details see Supplementary Note 1). Hence, there was strong evidence for the hypothesized increase of speciation rates in small-fruited vertebrate-dispersed palm clades relative to large, megafaunal-fruited palms, at least for the Old World.

Understory habitat. About 39% of all sampled palm species ($n = 802$ species) occur in the forest understory, and palms with small fruits are more common in the understory than palms with large fruits (91% and 9%, respectively). To quantify the relative importance of fruit size and understory habitat for speciation rates in palms (H2, Table 1), we used fruit sizes and additional data on understory habitat in a Multiple State Speciation and Extinction (MuSSE multistate) model[25]. We compared the additive and interaction effects of these two binary traits (small fruits and understory habitat) to a baseline MuSSE model that estimated speciation rates when both traits were absent, that is, relative to palm lineages that have large, megafaunal fruits and a canopy habit. Globally, the best-fitting MuSSE model indicated that both small fruits and understory habitat had a positive effect on speciation rates relative to the baseline (H2; Fig. 3a, compare yellow versus grey box-and-whisker plots). In addition, there was a positive interaction effect (red box-and-whisker plot, Fig. 3a), indicating that fruit size and understory habitat acted synergistically to increase speciation rates. Hence, understory palms with small fruits had the highest speciation rates at a global scale. As understory palm species are more common in the New World than the Old World relative to canopy species (45% and 36%, respectively), we further tested whether this interaction effect differed among these regions. In the New World, the best-fitting MuSSE model confirmed the global analysis, that is, both additive and interactive effects of small fruit size and understory habitat

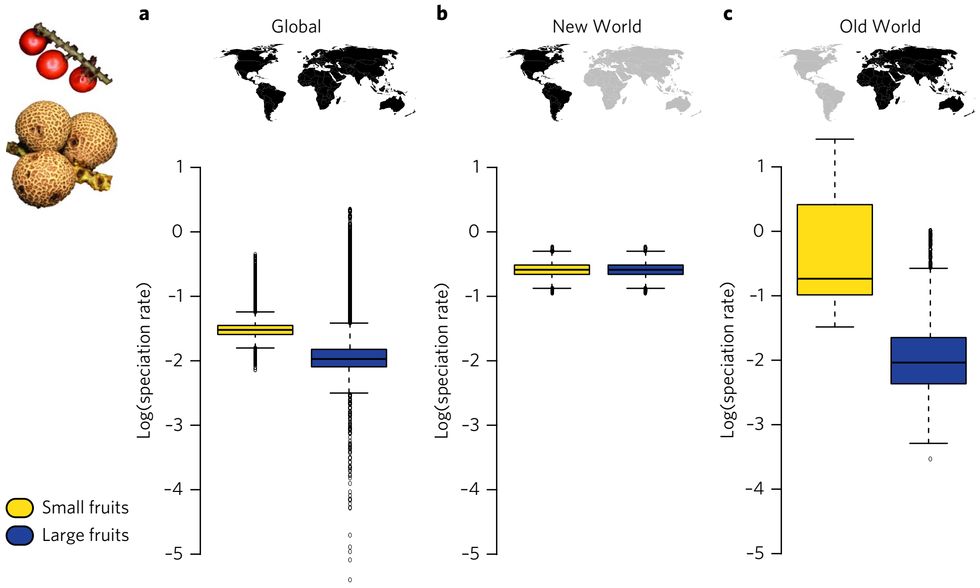

Fig. 2 | Speciation rate estimates for palm lineages with small (<4 cm) and large (≥4 cm) fruits. a–c, Rates are inferred globally (**a**) as well as separately for the New World (the Americas; **b**) and the Old World (Africa, Asia and Australia; **c**) using BiSSE models with 100 palm phylogenies. Box-and-whisker plots indicate the median, 1st and 3rd quartiles, and limits of the 95% Bayesian credibility intervals of the speciation rates as estimated through Bayesian MCMC methods. Outliers outside the 95% Bayesian credibility intervals are shown as dots. Small-fruited palm lineages show higher speciation rates than large, megafaunal-fruited palms globally (a 1.6-fold increase; median $\lambda_{\text{small}} = 0.22$, $\lambda_{\text{large}} = 0.14$) and in the Old World (a 3.4-fold increase; median $\lambda_{\text{small}} = 0.48$, $\lambda_{\text{large}} = 0.13$), but not in the New World (where the best model suggested an equal rate of both large- and small-fruited palms, see Supplementary Table 3).

were detected (Fig. 3b). However, in the Old World, only positive additive effects were supported, but no interaction term (Fig. 3c).

Island colonization. About 13% of all included palm species ($n = 331$ species) are restricted in their occurrence to oceanic islands, 80% are restricted to the mainland or to continental islands ($n = 2{,}036$ species), and 7% occur both on oceanic islands and mainland or continental islands ($n = 190$ species). As the latter group has the potential to colonize remote islands, we classified them here into the oceanic island category. Using MuSSE models, we tested whether small fruit size in combination with oceanic island colonization has an effect on speciation rates (H3, Table 1). At a global scale, the best-fitting MuSSE model for fruit size and island colonization indicated that small fruits and island colonization have both positive additive effects (Fig. 4a, compare yellow versus grey box-and-whisker plots) as well as positive interactive effects (red box-and-whisker plot, Fig. 4a) on speciation rates, compared with large, megafaunal-fruited palm lineages that are distributed on the mainland. Interestingly, in the New World, the best-fitting MuSSE model only supported positive additive effects of small fruit size and island colonization, but no interaction effect (Fig. 4b). Moreover, the posterior distributions of the speciation rates resulting from the Bayesian analysis strongly overlapped, suggesting only a slight increase in speciation rates due to small fruits and island colonization relative to large, megafaunal-fruited mainland palms (Fig. 4b). However, in the Old World, the results from the global analysis were confirmed (Fig. 4c), suggesting that small-fruited palm lineages on oceanic islands have particularly high speciation rates.

Discussion

Using trait-dependent diversification models and time-calibrated species-level phylogenies of palms, we show that dispersal-relevant traits are important drivers of palm radiations. Speciation rates were higher for palm lineages with small fruits (<4 cm in length) compared with large, megafaunal-fruited lineages (≥4 cm in length), especially in the understory of New World tropical forests as well as on Old World oceanic islands. These results suggest that plant speciation is enhanced by the evolution of small fruit sizes in conjunction with understory habitat and island colonization. This can be related to the dispersal and movement behaviour of particular frugivores, for example, the spatially restricted seed dispersal of small-bodied frugivores in the understory of rainforests or the seed dispersal to isolated islands by strong-flying frugivores that can cross oceanic barriers. These results suggest that frugivory-related traits are important drivers of speciation in vertebrate-dispersed plants[5]. They further demonstrate the importance of plant–animal interactions for the origin of tropical diversity[26].

Fruit size-dependent speciation. The hypothesis that small-fruited palms have a higher speciation than large-fruited palms (H1, Table 1) was supported in the global and Old World analyses (Fig. 2). In general, vertebrate-dispersed plants with small fruit sizes tend to be dispersed more frequently by small-bodied frugivores than by large-bodied frugivores[2,7]. As vertebrate body size scales with home range area, small-bodied frugivores on average have a more restricted space use than large-bodied frugivores[10,11]. As a consequence, small-fruited plants typically show frequent short-distance and rare long-distance dispersal events[3,27]. Large-bodied frugivores such as megafauna often show large-scale movements[17,28], which increases the frequency of long-distance dispersal events, particularly in large-fruited plants[2]. Dispersal distances of small-fruited vertebrate-dispersed plants therefore tend to be shorter than those of large-fruited plants, which results in lower gene flow among plant populations and therefore an increased probability of genetic differentiation and allopatric speciation[2]. Biogeographic comparisons of fruit sizes[6] and studies of disperser loss in tropical forest fragments[29] also support the idea that seed disperser body size imposes a strong selective pressure on fruit size. Our results provide macroevolutionary evidence that fruit size can have a strong influence on diversification dynamics of vertebrate-dispersed plants. The lack of an

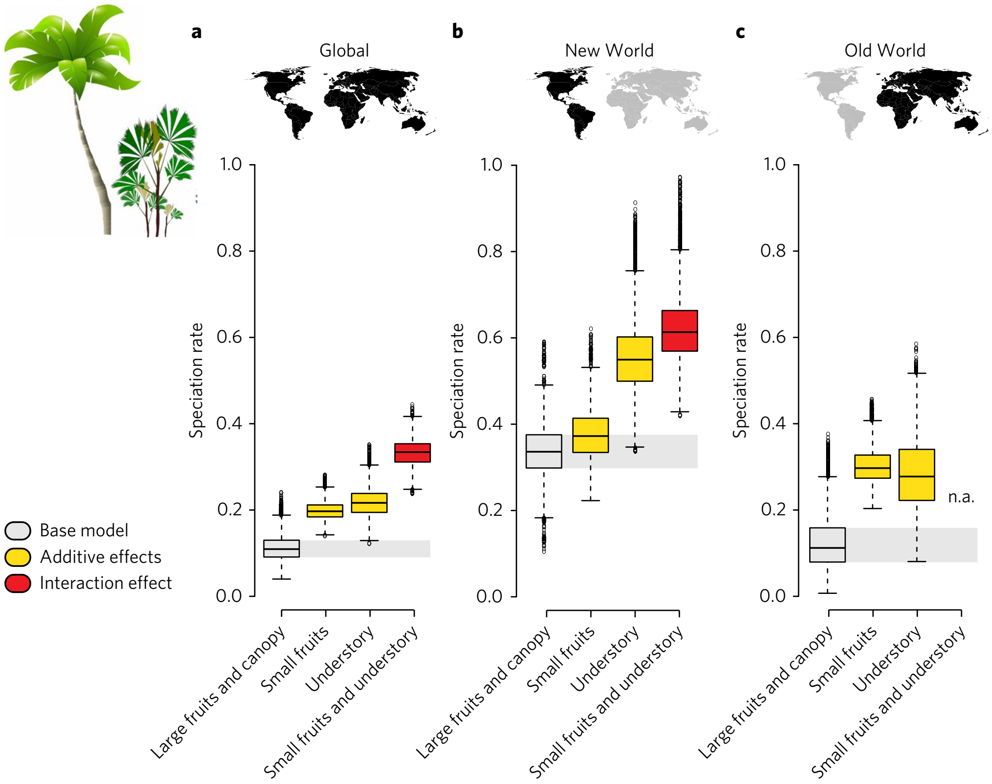

Fig. 3 | Understory habitat and its effect on speciation rates for palm lineages with small (<4 cm) fruits. a–c, Rates are inferred globally (**a**) as well as separately for the New World (the Americas; **b**) and the Old World (Africa, Asia and Australia; **c**) using MuSSE models with 100 palm phylogenies. Box-and-whisker plots indicate the median, 1st and 3rd quartiles, and limits of the 95% Bayesian credibility intervals of the speciation rates as estimated through Bayesian MCMC methods. Outliers outside the 95% Bayesian credibility intervals are shown as dots. The base model indicates rates of large, megafaunal-fruited (≥4 cm) canopy palms. Small fruits and understory habitat both add positively to the speciation rate compared with the base model. In the global and New World analyses, an interaction term was supported, suggesting the highest rates for small-fruited understory palms. No value is given for the interaction for the Old World as a model without it was preferred by AIC (indicated by n.a. (not applicable)).

effect of small fruit sizes on speciation rates in the New World might be influenced through the long-distance dispersal along rivers by fish. For example, South American fish species in the genus *Brycon* have been observed to disperse small-fruited palms (for example, *Oenocarpus bacaba*, *Astrocaryum jauari* and species of *Bactris*)[21]. However, to what extent this might have caused a decrease in speciation rates in palm lineages remains unclear.

Understory habitat. In support of the understory habitat hypothesis[4,16] (H2, Table 1), our results show that small fruit size in combination with understory habitat leads to exceptionally high speciation rates in palms, but only in the New World and not in the Old World (Fig. 3). Indeed, several Neotropical understory palm genera with small fruits (for example, *Chamaedorea* and *Geonoma*) have been mentioned in support of the understory habitat hypothesis[4]. These genera along with some other palm genera (that is, the node leading to *Desmoncus*, *Bactris* and *Astrocaryum*) represent a diversification rate shift across the palm phylogenetic tree[30]. Radiations of these palm genera could be, at least partly, driven by the spatially restricted movements of the many small-bodied understory frugivores in Neotropical forests[4,15]. For instance, many Neotropical understory birds show higher genetic differentiation than canopy birds, indicating low dispersal across biogeographic barriers such as rivers[13,31]. This limited dispersal of understory frugivores reduces gene flow and ultimately promotes speciation[2,14]. In the Old World, speciation rates of understory palms were also higher than those of large, megafaunal-fruited canopy palms, but no additional increase in speciation rates due to small fruit sizes was supported. This may be explained by the paucity of small-bodied, sedentary understory frugivores in the Old World[15,32] and because radiations of large-bodied, ground-living avian frugivores comparable to, for example, the New World cracids (Cracideae) and trumpeters (Psophiidae), are relatively rare in the Old World[32,33]. Furthermore, differences in speciation of small-fruited understory palms between the New World and the Old World may also be explained by the taller status of the Old World rainforests[34], potentially due to competition-driven selection for larger growth forms, or due to historical climate stresses, notably in Africa[35].

Island colonization. Many islands show spectacular palm radiations[35–37], suggesting that island colonization could be a major driver of palm speciation. Oceanic islands and island-like environments are characterized by restricted colonization and limited gene flow[4,18,38,39] that can increase speciation rates relative to the mainland or continental islands (H3, Table 1). Our results (Fig. 4) supported this hypothesis by demonstrating a particularly high speciation rate for small-fruited palm lineages on Old World islands. This result is primarily driven by palm diversification in Southeast Asia (95% of the Old World palm species occur in Indomalaya, Australasia, Pacific and the western Indian Ocean) rather than diversification on the relatively species-poor African continent. This was supported by a similar result when removing the Afrotropical species ($n=56$) from the analysis (Supplementary Fig. 2). The high diversity of palms on Old World islands[36,40] coincides with a high species richness of large-bodied, strong-flying avian frugivores in this region, especially the predominance of

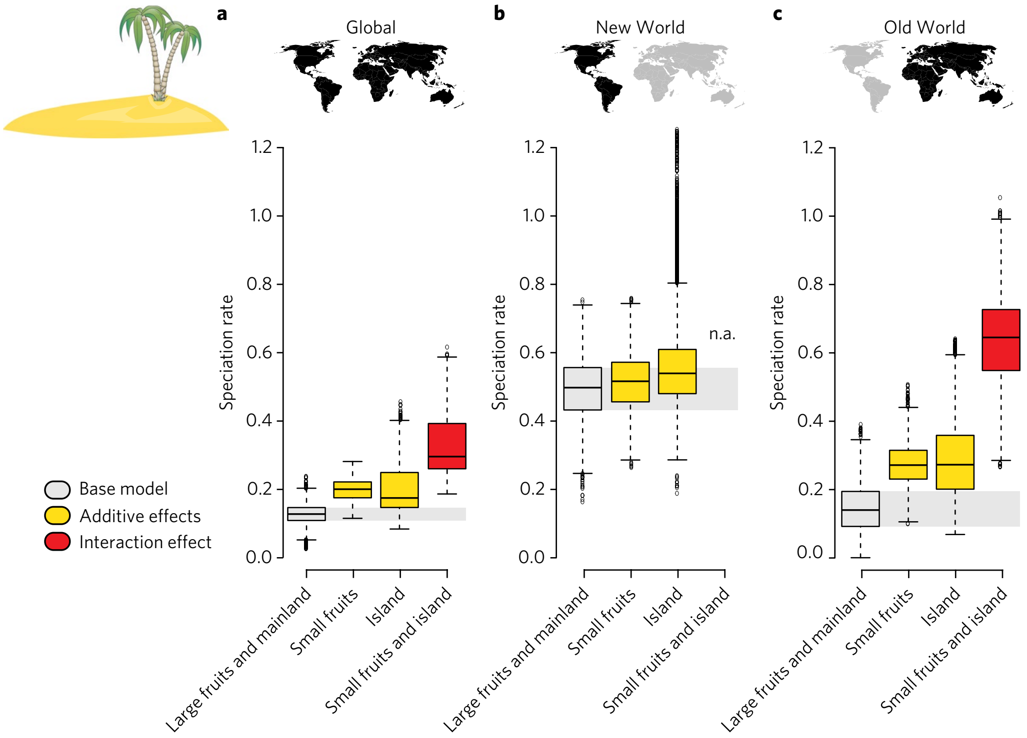

Fig. 4 | Island colonization and its effect on speciation rates for palm lineages with small (<4 cm) fruits. a–c, Rates are inferred globally (**a**) as well as separately for the New World (the Americas; **b**) and the Old World (Africa, Asia and Australia; **c**) using MuSSE models with 100 palm phylogenies. Box-and-whisker plots indicate the median, 1st and 3rd quartiles, and limits of the 95% Bayesian credibility intervals of the speciation rates as estimated through Bayesian MCMC methods. Outliers outside the 95% Bayesian credibility intervals are shown as dots. The base model indicates rates of large, megafaunal-fruited (≥4 cm) mainland or continental island-distributed palms. Small fruits and island distribution both add positively to the speciation rate compared with the base model. In the global and Old World analyses, an interaction term was supported, suggesting the highest rates for small-fruited island-distributed palms. No value is given for the interaction for the New World as a model without it was preferred by AIC (indicated by n.a. (not applicable)).

fruit pigeons (Columbidae) in Australasia and frugivorous hornbills (Bucerotidae) in Indomalaya[1]. These birds[38] as well as fruit bats (Pteropodidae)[12] successfully colonize remote islands and thereby contribute to long-distance seed dispersal of vertebrate-dispersed plants across oceanic barriers. Further empirical studies provide evidence of frequent long-distance seed dispersal of large-bodied birds at landscape and biogeographic scales[17,28] as well as of dispersal of palm fruits to remote islands[21,41]. Hence, the diversity of these frugivorous birds may have facilitated island colonization by palm lineages with relatively small fruit sizes (<4 cm, small enough to be swallowed by ocean-crossing frugivorous birds and bats) in the Old World. The lack of a relationship between speciation rates, fruit size and island colonization in the New World might be influenced by the dispersal behaviour of Neotropical birds. Many understory bird species that are widespread in Neotropical rainforests lack representatives on oceanic islands[31]. This could indicate that they refuse to disperse across water, which may have constrained the overall dispersal and subsequent radiation of Neotropical palms on oceanic islands.

Other potential drivers of palm radiations. Remarkable evolutionary radiations and exceptionally high diversification rates have been previously identified for various palm genera (for example, refs [19,30,35]). Such fast diversification might be driven not only by interactions with frugivorous vertebrates, but also by heterogeneity in topography, soils and microenvironments[42–44], long-term climate and biome stability[35], or other types of biotic interactions such as those with herbivores and pathogens[44]. A potentially confounding factor in terms of correlated evolution between fruit size and plant size[45] was not supported in our analyses because the negative association between fruit size and speciation remained after correcting for plant height (see Supplementary Note 1). Beyond fruit sizes, other fruit traits (for example, fruit colour, softness, odour and exposure) or defence traits (for example, spines) could also influence the diversification of vertebrate-dispersed plants[46–48]. Moreover, the former presence of a rich, now largely extinct megafauna (for example, extinct proboscideans, pilosans, cingulates and notoungulates) in the Neotropics would have influenced long-distance seed dispersal and gene flow of large-fruited palms[8,9], and may additionally explain some of the observed differences in diversification between New World and Old World small- versus large, megafaunal-fruited palms (see Supplementary Note 3).

Conclusions

Although several lines of evidence have previously been used to infer a potential role of frugivores in the diversification of vertebrate-dispersed plants (for example, refs [2,4,16,49]), rigorous quantitative tests of specific hypotheses in a phylogenetic framework have been limited[5], especially beyond sister clade comparisons[2]. Using a species-level phylogeny of palms combined with extensive trait datasets, we demonstrated that speciation rates of palms are highest in small-fruited palm lineages (<4 cm fruit size), especially in the understory of New World rainforests as well as in insular environments of Southeast Asia and the Pacific. In both systems, comparably small fruits probably promote the establishment of isolated populations through their interaction with particular frugivores. Considering the evolution of intrinsic traits (for example, fruit size, growth form) in interaction with geography (for example, oceanic islands) and the biotic environment (for example, frugivores and their movement behaviours) is therefore essential for understanding plant radiations[50]. The combination of time-calibrated phylogenies with ecological, interaction-relevant traits is thus particularly useful for gaining a deeper understanding of how biotic interactions have constrained or mediated the evolutionary radiations of plants.

Methods

Phylogeny. We used a recently published all-evidence species-level supertree of palms that includes almost all accepted palm species ($n = 2,539$)[22]. This time-calibrated, phylogenetic tree is based on a backbone generated from nine plastid and four nuclear markers as well as morphological data[51], and additional molecular and morphological data for several genera[22]. The phylogenetic tree was dated using five calibration points[20]. A Bayesian modelling approach was used to place species without genetic or morphological data in the phylogeny, based on taxonomy (for details see ref. [22]). As this leads to uncertainty in the exact placement of a species within the phylogeny, all analyses were performed on a set of 100 randomly sampled palm phylogenetic trees from the posterior distribution, available from ref. [22].

Data on fruit sizes. Information on fruit sizes was collected for a total of 1,836 palm species (ca. 70% of all palm species) from various sources, including primary literature, monographs, herbaria and palm websites (all sources are listed in Supplementary data sources). Specifically, we calculated the average fruit length for each species (based on multiple records per species, if available), because fruit length is the most commonly reported fruit size trait in monographs and species descriptions (see Supplementary Fig. 3 for fruit size frequency distributions). For the analyses, we classified species into two groups: small-fruited palms (fruits <4 cm in length) and large-fruited palms (fruits ≥ 4 cm in length). As palm fruits are usually single-seeded[19], the large-fruited palms represent species with 'megafaunal' fruits[8,9]. Across the palm family, at least 229 palm species have large, megafaunal fruits (Fig. 1), and about one-third of the palm genera have at least one species with such fruits (Supplementary Table 1). We used the binary state of fruit size (small or large) rather than a continuous variable because the implemented diversification models (see below) deal with binary data, and because species with large, megafaunal fruit sizes are dependent on seed dispersal by large-bodied mammalian frugivores (megafauna), thereby excluding volant frugivores (birds, bats) and small- and medium-sized frugivores. In contrast, species with small fruit sizes are predominantly ingested by birds and small- and medium-sized mammalian seed dispersers[2].

Data on understory habitat. To quantify affiliation with the forest understory, we compiled species-level data on maximum stem height for 2,073 palm species (ca. 81% of all palm species) from the same sources as used for the fruit size data (see Supplementary data sources). For all palm species, we additionally determined their main growth form (climber, acaulescence, erect shrub/tree). From these data, we estimated whether palms present their fruits in the understory. This included short-stemmed palms (maximum stem height ≤ 5 m) as well as all acaulescent species (that is, having no or only a very short stem concealed in the ground). Palms with a stem height >5 m were considered to be non-understory plants, that is, tall-stemmed or medium-sized palms and most climbers (referred to as 'canopy').

Data on island colonization. The palm family has a pantropical distribution (that is, it occurs in all tropical regions). To quantify species distributions on islands, we compiled global presence–absence data for all palm species from the world checklist of palms[52]. This exhaustive, authoritative checklist records palm species occurrence within level 3 geographic units as defined by the International Working Group on Taxonomic Databases (TDWG) (referred to as 'botanical countries')[52]. These generally correspond to countries, although larger countries such as the United States are normally broken down into smaller political units. Palm occurrence data are freely available from the continuously updated World Checklist of Monocotyledons (http://apps.kew.org/wcsp), and we here used a database version downloaded in July 2015. For our analyses, we defined a binary state (island or mainland) describing whether a species occurs on volcanic and atoll islands (referred to as 'island'), or on the mainland or on continental islands (referred to as 'mainland'), following the classification from ref. [53]. This classification follows geology as a surrogate for isolation, in which oceanic and atoll islands have arisen as newly formed land, whereas continental islands are either part of the continental shelf or were once connected to continental landmasses (for example, Madagascar). The occurrence of palm species on oceanic and atoll islands consequently must have resulted from colonization and speciation in isolation, whereas palm lineages on continental islands have experienced less isolation. This classification closely matches the classification based on the connectivity of islands to the mainland during the last glacial maximum, as quantified by ref. [54].

Performance of trait-based models. In this study, we tested the impact of specific traits on the diversification of lineages using the maximum likelihood based 'state speciation and extinction' or 'SSE' models[24,55]. These methods calculate the probability that a lineage evolved as observed given a model of character evolution. However, SSE models have recently been criticized for high type I error rates[56], suggesting that a significant effect of a trait on speciation rates can be detected even if it is not truly present. We evaluated this bias by performing simulations in which neutral binary traits evolved on 100 empirical palm phylogenies[22] under several transition rate scenarios, as recommended by ref. [56].

These simulated (neutral) binary traits are expected to be neutral with respect to speciation rates. We evaluated the Bayesian credible intervals in speciation rates between these simulated binary traits after running a Bayesian Markov chain Monte Carlo (MCMC) for 10,000 generations on the 100 palm phylogenies. Our results showed a strong overlap of Bayesian credible intervals between character states on speciation rates under all transition rate scenarios (Supplementary Fig. 4), supporting the expectation that these neutral traits do not affect speciation rates in palms. This suggests that the empirical results can be reliably obtained from the 'SSE' models. In addition, our dataset meets the other requirements for applying SSE models, such as sufficient replication events (for example, the independent evolution of small fruit sizes)[57], >300 species and balanced character state distributions (that is, no fewer than 10% of one character state)[58] (for more details on these simulations see Supplementary Note 2).

Fruit size-dependent speciation. We used the BiSSE model[24,55] implemented in the 'diversitree' package[25] in R[59] to model speciation (λ), extinction (μ) and transition (q) rates of small-fruited versus large, megafaunal-fruited palm lineages (H1 in Table 1). The BiSSE model jointly estimates speciation, extinction and transition rates of a binary trait by using dated phylogenetic trees, and trait states assigned to the species at the tips of the trees. We focus on speciation rates because our hypotheses (Table 1) directly refer to speciation rather than extinction or net diversification. Nevertheless, the joint estimation of these rates is desirable as trait changes may not be independent from speciation and extinction rates[55]. We report and discuss all evolutionary rates other than speciation in Supplementary Note 3 and Supplementary Fig. 5, and provide an overview of the model selection globally as well as for the New World and Old World, respectively (Supplementary Tables 2–4). We fitted eight BiSSE models with decreasing complexity (parameters) and selected the best-fitting models based on likelihood-ratio tests under a Chi-square distribution and Akaike's information criterion (AIC) (Supplementary Tables 2–4). These models included constraints on speciation, extinction and transition rates between trait states[24]. Maximum likelihood was used to optimize full and constrained models. BiSSE enables correcting for species and their traits not sampled in the datasets by indicating a sampling fraction, that is, 32% of small-fruited and 18% of large, megafaunal-fruited palm species were not sampled in the global dataset. This fraction was based on imputed trait values from the PhyloPars algorithm[60] for those species sampled in the phylogenetic tree but lacking fruit size data (these inputed trait values were only used to calculate sampling fractions, not in the actual analyses). A MCMC was run for the best-fitting model for 10,000 generations on 100 randomly sampled palm phylogenies. We evaluated the posterior distribution of these Bayesian rates, and in case the 95% Bayesian credibility intervals between parameter states did not overlap, we considered them significantly different from each other[24].

All analyses were run globally as well as separately for the New World (including South, Central and North America as well as the Caribbean) and the Old World (including Australia, Indomalaya, Oceania, Pacific, Africa, Madagascar and surrounding islands). This geographic division was used because most palm species (as well as genera) are endemic to one of these regions[35]. Hence, these regions are characterized by distinct historical differences in terms of palm diversification[30,61], frugivore communities[1], and representation of understory palm species (45% and 36% in the New World and Old World, respectively) and island-distributed palm species (8% and 28% in the New World and in the Old World, respectively).

As results may be biased by the allometric relationship between fruit size and plant size, we repeated the analyses after accounting for the correlation between palm maximum stem heights and fruit sizes. The effect of residual fruit sizes (after correcting for maximum plant height) on speciation rates was assessed with BiSSE (for details on the approach see Supplementary Note 1, for model selection see Supplementary Table 5 and for results see Supplementary Figs. 1 and 5). However, as these residuals do not represent 'true' small and large fruits, we also investigated the effect of residual fruit sizes on speciation rates using the Quantitative Speciation and Extinction (QuaSSE) model[62]. QuaSSE can be used to test the effect of a continuous trait on speciation rates by testing the fit of models describing the distribution of the response (that is, speciation rate) to the trait (for example, constant, linear or sigmoidal). Details on the methods and results of this analysis are provided in Supplementary Note 1, Supplementarty Table 6 and Supplementary Fig. 6.

Furthermore, to test whether our binary classification of fruit size biased the results, we additionally tested the effect of fruit size as a continuous trait on speciation rates. We first estimated speciation rate heterogeneity across the phylogeny with a Bayesian Analysis of Macroevolutionary Mixtures (BAMM)[63] and then compared the observed difference in speciation rate between palms that exhibit different fruit sizes to a background speciation rate through randomizing the estimated tip speciation rates from the BAMM outputs[64]. These additional analyses also confirmed the high speciation rate of small-fruited palm lineages. Details on the methods and results of this analysis are provided in the Supplementary Note 4 and Supplementary Fig. 7.

Speciation rates due to understory habitat and island colonization. The effects of a trait (for example, fruit size) on speciation rates may be enhanced by an interaction effect with another trait. For example, palms in the understory or on islands may have particularly high speciation rates if they have also small fruits. To disentangle such effects, we implemented the MuSSE multistate model[25]. The MuSSE model can be used to quantify the additive and interactive effects of two binary traits (for example, small fruit size and understory growth form, or small fruit size and island colonization) on speciation, extinction and transition rates. The model intercept of the MuSSE model (the 'base model') estimates speciation rates when both traits are absent (for example, palm lineages with large, megafaunal fruits that do not grow in the understory). The interaction term (when both traits are present) will indicate whether these traits may interact in either a positive way (that is, both traits increase speciation rates) or a negative way (that is, both traits decrease speciation rates).

To quantify trait-dependent diversification for both binary trait combinations (H2: small/large fruit size and understory/canopy habitat; H3: small/large fruit size and island/mainland distribution), we compared the likelihood of a total of 16 models with increasing complexity (Supplementary Table 7). We used stepwise AIC model selection, globally as well as separately for the New World and Old World, and selected the models with the lowest AIC (Supplementary Tables 8 and 9). A MCMC for the best-fitting model (based on AIC) was run for 10,000 generations on 100 palm phylogenies. We tested for the additive and interactive effects of small fruits and understory habitat (compared with large, megafaunal-fruited canopy palms) on speciation rates (Supplementary Table 8), and between small fruits and oceanic island colonization (compared with large, megafaunal-fruited mainland/continental island-distributed palms) on speciation rates (Supplementary Table 9). We report and discuss all evolutionary rates other than speciation rates in Supplementary Note 5 and Supplementary Fig. 8.

Data availability. The phylogenetic data that support the findings of this study are available from ref. [22] and the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.cm4nm. The palm species distribution data are available from the World Checklist of Selected Plant Families (http://apps.kew.org/wcsp). The BiSSE and MuSSE scripts and the palm trait data to perform the analyses in this study are available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.cm4nm. An extended palm trait dataset is currently prepared for publication as a data paper.

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Author contributions

W.D.K. conceived the idea; W.D.K. and R.E.O. designed the study; W.D.K. and R.E.O. collected data; R.E.O. analysed the data; R.E.O. and W.D.K. wrote the manuscript; all authors discussed the results and commented on the manuscript.

Competing interests

The authors declare no competing financial interests.

Additional information

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Experimental design

1. Sample size

Describe how sample size was determined.	The sample size used in this study was determined based on the species richness in the palm family, i.e. 2539 species. Ideally, all species would be included in the analyses. However, as we combined the completely-sampled phylogenetic data with our trait databases, only ca. 70% of the species could be included. We were not able to obtain trait data for the remaining 30% of the species. Nevertheless, a sample size of ca. 1836 species is sufficient to test the proposed hypotheses with trait-dependent diversification models as done in this study. This sample size is large compared to similar studies combining phylogenetic and trait data.

2. Data exclusions

Describe any data exclusions.	No data were excluded in this study.

3. Replication

Describe whether the experimental findings were reliably reproduced.	No experiments were performed in this study. The replication in this study is reflected by replicated evolutionary events, e.g. the independent and replicated evolution of large, megafauna fruits, and the associated decreases in speciation rates. Although we cannot precisely say how many times this happened, and thus the exact number of replicates, large fruits occur in at least 63 our of 183 palm genera, and this could suggest that the evolutionary transition from large to small fruits or vice versa happened 63 times, thus indicating 63 replication events.

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.	Our experimental groups are large-fruited and small-fruited species. These groups were determined based on the ecology and expected seed dispersers feeding on species with these fruit types. This allocation was thus non-random. However, to test the robustness of the results, all analyses were repeated using simulated, random data. This allows for a comparison between observed results on differences between groups, to the randomized results.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.	Blinding was not relevant to the study here, as inferences of the past are made, rather than experimental approaches at present. As the past is our experimental setup, the inferences made are independent of the investigator. All analyses can be repeated using scripts available on request from the corresponding author.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or the Methods section if additional space is needed).

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☒	☐	A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly.
☒	☐	A statement indicating how many times each experiment was replicated
☐	☒	The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
☐	☒	A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☐	☒	The test results (e.g. *p* values) given as exact values whenever possible and with confidence intervals noted
☐	☒	A summary of the descriptive statistics, including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
☐	☒	Clearly defined error bars

See the web collection on statistics for biologists for further resources and guidance.

Software

Policy information about availability of computer code

7. Software

Describe the software used to analyze the data in this study.	All analyses were performed in the R environment: R Development Core Team. R: a language and environment for statistical computing, version 604 3.1.0 (2014-04-10), <http://www.R-project.org> (2014).

For all studies, we encourage code deposition in a community repository (e.g. GitHub). Authors must make computer code available to editors and reviewers upon request. The *Nature Methods* guidance for providing algorithms and software for publication may be useful for any submission.

Materials and reagents

Policy information about availability of materials

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.	The trait database used in this study is available from the authors (W.D.K.) on reasonable request. However, we are currently in the process of publishing this trait database as a separate data paper, which will be accomplished before the ending of project grant 824.15.007 by the Netherlands Organisation for Scientific Research to W.D. Kissling, finishing in May 2019. This trait database will then be openly accessible to anyone interested in using it.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).	No antibodies were used.

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.	No eukaryotic cell lines were used.
b. Describe the method of cell line authentication used.	No eukaryotic cell lines were used.
c. Report whether the cell lines were tested for mycoplasma contamination.	No eukaryotic cell lines were used.
d. If any of the cell lines used in the paper are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.	No eukaryotic cell lines were used.

Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.	No animals were used.

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.	The research did not involve human research participants.