Ecological and evolutionary significance of primates’ most consumed plant families

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Angiosperms have been essential components of primate diets for millions of years, but the relative importance of different angiosperm families remains unclear. Here, we assess the contribution and ecological and evolutionary significance of plant families to diets of wild primates by compiling an unprecedented dataset of almost 9000 dietary records from 141 primary sources covering 112 primate species. Of the 205 angiosperm plant families recorded in primate diets, only 10 were consumed by more than half of primate species. Plants of the Moraceae and Fabaceae families were the most widely and frequently consumed, and they likely represent key-stone resources for primates. Over 75% of species fed on these two families, and together they made up a median of approximately 13% of primate diets. By analysing the relative proportion of different plant parts consumed, we found that Moraceae was mainly eaten as fruit and Fabaceae as non-fruit parts, with the consumption of these two families not showing a significant phylogenetic signal across primate species. Moraceae consumption was associated with small home range sizes, even though more frugivorous primates tended to have larger home ranges compared to more folivorous species, possibly due to the year-round availability of moraceous fruits and the asynchrony in their phenology. Our results suggest that primates may be intricately and subtly shaped by the plant families that they have consumed over millions of years, and highlight the importance of detailed dietary studies to better understand primate ecology and evolution.

1. Introduction

Tropical angiosperms have been a major source of nutrition for primates throughout their evolutionary history [1]. Almost all of the more than 500 extant primate species [2] are highly dependent upon the fruits, leaves, seeds, flowers, nectar, bark, and other parts of flowering plants to meet their energetic and nutritional demands for survival, growth, development and reproduction [3–5]. Consequently, primates may have co-adapted with angiosperms, particularly with those plant families they have interacted with most intensely over time [6]. This dependence and apparent competition for angiosperm food resources has likely also shaped phylogenetic patterns in diet across the primate family, where even closely related lineages may vary greatly in dietary specialization (e.g. obligately frugivorous chimpanzees versus opportunistically frugivorous gorillas). Thus, the evolution of primates is intrinsically interconnected with the evolution of angiosperms over the last 55 million years [7–9], and the mutu-
As a consequence, more frugivorous primates tend to target daily protein thresholds, while more folivorous species tend to target daily caloric thresholds [11,12]. As fruit resources may be spatially and temporally patchy, more frugivorous species tend to have larger home range sizes compared to more folivorous species [1]. Furthermore, primates with more folivorous diets tend to have a larger body size to cope with the high fibre content of their diets, given their large guts that allow them to more effectively digest their cellulose-rich diets and more efficient metabolism to subsist on lower quality foods [13,14].

While much is known about the role of plant parts and nutritional content from local field studies of primate dietary ecology, no large-scale synthesis of the taxonomic composition of primate diets is available. Studying the relative proportion of different plant families in primate diets may reveal important insights into how variation in plant morphology and chemistry, including nutrients, toxins and other secondary compounds, across plant species, genera and families relates to variation in primate physiological, morphological and behavioural traits. For example, the leaves and seeds of Fabaceae tend to be higher in protein content compared to other plant families due to the ability of most species in the family to fix nitrogen [15]. Such phylogenetic conservatism in traits at the plant family level [16] similarly extends to toxic secondary compounds (e.g. tannins, alkaloids), which may require special adaptations that allow primates to circumvent these defences. Primate traits may also be shaped by the temporal and spatial availability of resources provided by different plant families (e.g. phenology of fruiting, size of fruit crop).

We compiled a novel global dataset of wild primate diets to synthesize our knowledge of primate’s use of plant families and their parts (e.g. fruit, leaf). For widely consumed plant families, we tested for phylogenetic patterns in consumption across primate taxa and to what extent the consumption of these families was associated with primate dietary specialization, home range size and body mass. We hypothesized that (i) only a few plant families would form a core component of primate diets, while most others would be consumed to a small degree, with different plant families used for different parts, given variation in availability and phytochemistry; (ii) a phylogenetic signal would exist in plant family consumption given dietary variation across primate lineages (e.g. folivorous colobines will consume high amounts of legumes given their high protein content of leaves) and (iii) the most consumed plant families would influence primate traits such as body mass and home range size given their importance in terms of availability and phytochemistry. Although other primate dietary databases exist (e.g. [17]), we are not aware of any open-access dataset that covers the full breadth of the primate phylogeny with specific descriptions of food items for each plant family and their parts.

2. Material and methods
(a) Compilation of primate dietary data from the literature
To evaluate the relative contribution of different plant families across wild primate diets, we compiled quantitative studies of diet composition across primate species using a structured literature search. We obtained a preliminary set of articles using Web of Science in May 2019 using the following search terms: ‘(Food* OR Feed* OR Diet*)’. We started with articles that were published in four well-known primate journals (i.e. American Journal of Primatology, International Journal of Primatology, Folia Primatologica, and Primates), resulting in 2091 candidate articles. This initial search resulted in dietary studies for 71 primate species, which we further supplemented with references from a recently compiled primate trait database paper [17], as well as an expanded search to increase the taxonomic coverage of our database. The title and abstracts of articles were then screened using the R package ‘metafor’ [18]. Only articles that contained dietary studies with a quantitative and taxonomic breakdown of plant food items were considered. We defined a study as any quantitative summary of the diet based on direct observations of a population or group of a primate species over a discrete time period. Our criterion thus excluded studies that relied on indirect measures such as faecal sampling or metabarcoding approaches. When data from multiple populations or groups of a primate species or multiple species were reported in a single reference, we treated them as separate dietary studies.

All dietary records for plant and non-plant food items reported in each study were compiled. For dietary records of plant food items, we additionally recorded the taxonomic identity (plant genus and species names) and plant part (e.g. leaves, fruits) if provided (e.g. ‘Ficus natalensis young leaves’). Each dietary record was defined as the amount of time spent feeding on a given food item as a percentage of the overall amount of time observed feeding, the number of times a population was recorded feeding on a given dietary item as a percentage of the total number of feeding events observed, or an estimate of the relative weight of consumption compared to all items consumed, depending on the methodology of each study (e.g. [4]; electronic supplementary material, table S1). Diets were typically quantified either using scan or continuous sampling techniques (e.g. [19]).

Our dataset consisted of dietary information on 119 primate species, derived from 9270 dietary records across 232 studies in 149 references (electronic supplementary material, table S1). However, we omitted studies for which (i) the sampling period was shorter than six months in duration (to capture seasonal variation), (ii) the majority of the diet (greater than 50%) was not known or reported or (iii) the plant family for the majority of the plant portion of the diet (greater than 50%) was either not identified by the author(s) of the study or could not be taxonomically verified by us during collation. The filtered dataset comprised dietary records of 112 primate species across 220 studies from 141 references. Studies of primate species were geographically extensive and were distributed across Central and South America, the African continent, Madagascar and Asia (electronic supplementary material, figure S1). The median duration of studies in the filtered dataset was 12 months (s.d. = 8.7, range = 6–66). For the majority of primate species, dietary information was derived from only one study (s.d. = 1.3; 60 out of 112 species). For the remaining, dietary information of primate species was derived from between two to eight separate studies.

Of the 8981 dietary records in the filtered dataset, 8744 are associated with plants. Of these, 84% contained information on the plant part consumed. Of those dietary records (n = 7327), a total of 45 unique plant part terms were reported, sometimes in combination with many records (e.g. fruits and leaves). The large majority of plant parts identified were associated with leaves (n = 3198) and fruits (n = 3295), although a large number of records (n = 2913) was associated with other plant parts, including seeds and flowers (electronic supplementary material, table S2).

(b) Relative consumption of plant families
Taxonomic identity for each plant dietary item was standardized against Plants of the World Online [20]. To quantify the relative
importance of each of the plant families, we calculated the proportion of primate species that consumed each plant family. For all families consumed by more than 50% of primate species, we additionally quantified the percentages of each family (regardless of plant part) in the diet of each primate species (averaged across multiple studies of the same species) and the relative consumption of different plant parts (leaf, fruit and other) for each plant family (for more methodological details, see supplementary material and electronic supplementary material, figure S2).

(c) Phylogenetic conservatism in plant family consumption

To evaluate if closely related primate species would feed on a given plant family to a similar degree, we tested if the consumption of the widely consumed plant families (by more than 50% of primate species) showed a phylogenetic signal across the primate phylogeny. We analysed the average dietary percentages (regardless of plant part) for these families by calculating Pagel’s λ [21] and Blomberg’s K [22], two of the most widely used measures of the phylogenetic signal [23,24]. For both Pagel’s λ and Blomberg’s K, values of 0 indicate that the degree of consumption in a given plant family was random with respect to phylogeny, whereas values at or above 1 indicate that consumption was at or greater than expected under a Brownian motion model. We additionally analysed the occurrence of each of the widely consumed families in the diet (yes or no) using a binary measure of phylogenetic signal, D, which is based on a Brownian threshold model [25]. This allowed us to test if consumption of any given family was more likely within closely related primates, regardless of the degree of consumption actually observed.

To perform our tests of phylogenetic conservatism, we generated the maximum clade credibility tree using the posterior distribution of phylogenies provided by [26], using TreeAnnotator v. 1.10.4 [27]. Species names in our database were first reconciled with tip labels of the tree using the Integrated Taxonomic Information System database (www.itis.gov) and the IUCN (IUCN v. 3, 2019). In total, 108 out of the 112 primate species in the filtered dataset were represented in the phylogenetic tree. Pagel’s λ and Blomberg’s K, including significance tests, were performed using the ‘phylodisg’ function of the ‘phytools’ R package v. 0.6-99 [28]. D and significance tests were performed using the ‘phylod’ function of the ‘caper’ R package v. 1.0.1 [29]. For each test, correction for multiple testing [30] was performed using the ‘p.adjust’ function in R.

(d) Ecological and evolutionary correlates of frugivory and folivory

We estimated the degree of frugivory and folivory for each primate species using the same approach used for calculating the relative proportion of different plant part categories for each plant family: we calculated the average dietary percentages for each plant part category for each primate species (n = 97; see electronic supplementary material, figure S3). Supporting the reliability of our dataset and approach, our estimates of frugivory and folivory were highly congruent with two widely used trait databases that semi-quantitatively score the degree of frugivory and folivory from the natural history literature, EltonTraits [31] and MammalDiet [32] (see electronic supplementary material, figures S4 and S5).

We used structural equation models (SEM) [33] to evaluate potential causal relationships between the degree of frugivory or folivory, home range size and body mass. This was performed for 92 primate species for which estimates of both home range size and body mass were available [17]. Body mass estimates were an average of both sexes. Home range size and body mass were log-transformed. Where multiple estimates of either home range size and body mass were available, the average was used. Because we were interested in the role of the most important plant families in mediating these relationships, we additionally quantified the taxonomically identified proportion of either the leaf or fruit diet that was made up by the most consumed plant family for these two dietary categories (family percentage). We created two SEMs, one for frugivory and one for folivory, and both included three main components: (i) home range size as a response variable, with body mass, degree of frugivory or folivory, and family percentage as dependent variables, (ii) body mass as a response variable and degree of frugivory or folivory as well as a family percentage as dependent variables and (iii) a hypothesized path where family percentage was a function of the overall degree of frugivory or folivory. Because relationships may be driven by phylogenetic conservatism in traits (e.g. body mass, degree of frugivory/folivory due to dietary adaptations), the three SEM components (corresponding to linear regression models) were alternatively fitted using phylogenetic generalized least-squares (PGLS) models using the ‘gls’ function from the ‘nlme’ R package v. 3.1-140, [34]) with the correlation argument set using the ‘corBrownian’ function from the ‘ape’ R package v. 5.3, with the ‘gamma’ parameter set to 1. This approach assumes that the correlation between points is consistent with a Brownian model on the phylogenetic tree. We omitted two species in our phylogenetic SEM as they were not in the phylogenetic tree. Non-phylogenetic SEMs were implemented using the ‘lavaan’ R package v. 0.6-5 [35]. Phylogenetic SEMs were constructed from component PGLS models using the piecewiseSEM R package v. 2.1.0 [36].

3. Results

(a) Relative consumption of plant families

Across the 112 primate species from the filtered database covering 141 publications on primate diets, 205 angiosperm families were recorded (figure 1a), out of the approximately 416 angiosperm families worldwide [37]. Plant parts consumed included fruits, leaves, seeds, flowers and other items (e.g. exudates, tubers, bark) (electronic supplementary material, table S2). However, most of these 205 plant families were consumed by a limited number of primate species, with only 10 families being consumed by more than half of all species (figure 1b). Most families only had one or two genera (and four species or fewer) recorded. In general, only a few genera made up the most species recorded in each family. The three genera with the greatest number of species consumed were Ficus (Moraceae, 114 species), Pouteria (Sapotaceae, 40 species) and Inga (Fabaceae, 38 species) (electronic supplementary material, figure S8). Moraceae and Fabaceae were the two most consumed plant families in terms of both the number of primate species documented to consume at least one food item from that family and median percentage of diet across all diets. Out of the 112 primate species in our final database, 91 were observed feeding on Moraceae (81.3%) and 88 on Fabaceae (78.6%), while the median percentage of Moraceae and Fabaceae across primate diets was 7% and 6%, respectively (electronic supplementary material, table S3). Consumption of different plant families was also associated with different plant parts. Fruits of Rubiaceae, Moraceae, Sapotaceae, Myrtaceae and Anacardiaceae were consumed to a greater degree than their leaves (ratio of fruit: leaf consumed greater than 1.5), whereas only leaves of Fabaceae were consumed more than fruits (ratio of leaf: fruit consumed greater than 1.5) (figure 1c).
Phylogenetic conservatism in plant family consumption

The degree of consumption was random with respect to the phylogeny of primates for plant families consumed by at least half of the primate species (electronic supplementary material, table S3). A phylogenetic signal was also not detected when we considered the occurrence of consumption (binary variable; ‘yes’ or ‘no’) for most plant families. However, there was one exception. The occurrence of Fabaceae ($D = 0.57$, $p = 0.03$) consumption showed some non-random phylogenetic signal (i.e. $D < 1$), although such a signal was fairly weak and not as strong as that expected under a Brownian threshold process (i.e. $D = 0$).

Ecological and evolutionary correlates of frugivory and folivory

Across primates with data on plant parts consumed ($n = 97$), fruits were the most consumed item (median = 36%, s.d. = 25%, range = 0–92%), followed by leaves (median = 17%, s.d. = 27%, range = 0–92%), others (e.g. seeds, flowers) (median = 14%, s.d. = 19%, range = 0–88%) and animals (median = 0%, s.d. = 10%, range = 0–59%). A median of 5% of primate species diet was unidentified or not reported (s.d. = 12%, range = 0–50%; electronic supplementary material, figure S3).

For our analysis of the potential influence of plant families on primate traits, we focused on Moraceae fruits and Fabaceae leaves (figure 2b,c), as they were identified as the two most widely consumed plant families that formed a disproportionately large proportion of the fruit and leaf diets of primates, respectively. In our SEM, we found that frugivory primarily influenced home range size indirectly through a negative effect on body mass (path coefficient = $-0.344$, figure 3a,b). The more frugivorous a primate species, the smaller their body mass and thus the smaller their home ranges. The proportion of Moraceae in the fruit diet had a significant direct negative effect on home range size (path coefficient = $-0.253$), suggesting that with the degree of frugivory being equal, primate species that consume a greater proportion of Moraceae fruits are associated with smaller ranges.

Figure 1. Relative consumption of plant families across primate diets. A total of 205 plant families were recorded across the diets of 112 primate species. (a) Proportion of primate species consuming each plant family with the 10 families that were consumed by more than 50% of primate species highlighted in red. (b) Proportion of primate diets that came from the 10 families that were consumed by more than 50% of primate species regardless of plant part (displayed in descending order). Bold black lines represent the median percentage across all primate species, boxes represent the interquartile range and points represent species that were more than 1.5 times the interquartile range. (c) Relative proportion of different plant parts for the 10 families that were consumed by more than 50% of primate species (displayed in descending order), averaged across the diets of primate species recorded to consume them. ‘Others’ represents dietary records from the ‘seeds’, ‘flowers’, and ‘others’ categories (electronic supplementary material, table S2). (Online version in colour.)
home ranges, independent of body mass. After correcting for phylogeny, body mass was still correlated with home range size, but the effect of frugivory on body mass (path coefficient = $-0.109$) and the effect of Moraceae on range size (path coefficient = $-0.125$) were no longer statistically significant (figure 3b). However, under this model, frugivory had a significant positive correlation with Moraceae fruit consumption (path coefficient = 0.384).

Folivory was positively associated with larger body mass (path coefficient = 0.409) but negatively associated with home range size (path coefficient = $-0.446$), while body mass was associated with larger ranges (path coefficient = 0.668, figure 3c). This meant that body size kept equal, the more folivorous a primate, the smaller its home range size. However, the effect of folivory on body mass was not significant in the phylogenetic analysis (path coefficient = 0.076). The proportion of Fabaceae leaves in the leaf diet had no effect on either body mass or home range size in either model (figure 3c).

4. Discussion

(a) General trends in consumption of plant families across primate diets

Using an unprecedented dataset covering the relative contribution of all plant families in the diets of more than 100 species of primate worldwide, we show that primates consume a wide range of dietary items, including fruits, leaves, seeds, exudates, tubers, bark and flowers, from at least 205 plant families. However, only 10 plant families were consumed by more than half of the primate species. The largest component of primate diets was fruit (about 38% of diet), followed by leaves (about 26%), with fruit being the most consumed plant part within seven of the 10 widely consumed families: Moraceae, Sapotaceae, Rubiaceae, Anacardiaceae, Apocynaceae, Myrtaceae and Sapindaceae. By contrast, the only widely consumed family to be mainly consumed as leaves was Fabaceae.

All consumed plant families showed large variation in their importance to specific primates. Most families were consumed at low levels across the primate order and only highly consumed by a few primate species. For example, the third most widely consumed family, Sapotaceae, was eaten by 66% of species, but only made up greater than 10% of diet for 17 species. For one specific primate, the highly folivorous Preiss’ red colobus (*Piliocolobus preussi*), Sapotaceae plant parts composed almost 30% of the diet (electronic supplementary material, table S4). This extreme variation in consumption patterns for these plant families across primate species is probably due to a combination of the relative availability of different plant families in different geographic areas at both local and regional scales, variation in phytochemistry and morphology of various parts of particular plants in those areas, and the dietary adaptations of the primate species. One limitation of our dataset is that interannual and intergroup variation may not be fully captured for some species. Most species had only one study that was conducted over a period of greater than six months, highlighting the need for future dietary studies to track multiple primate populations over multiple years.

Nevertheless, the consumption of Moraceae and Fabaceae emerged as highly prevalent components in primate diets (in
Figure 3. Structural equation models depicting relationships between primate diets and traits. (a) Phylogenetic distribution of primate trait variation and diet depicted by a heat map. Colours represent standardized values (z-values), defined as the number of standard deviations that a value is away from the mean value of each trait (dark red indicating higher than average values whereas dark blue indicated lower than average values). (b) Structural equation model illustrating the relationships between primate body mass, home range size, degree of frugivory and % Moraceae fruits in the diet. (c) Structural equation model illustrating the relationships between primate body mass, home range size, degree of folivory and % Fabaceae leaves in the diet. Arrows represent direct effects with standardized path coefficients from non-phylogenetic SEMs above and PGLS models in parentheses below. Statistically significant relationships are marked with an asterisk (*) with red representing a negative relationship and green a positive relationship. For each response variable, the amount of explained variance ($R^2$) is given. (Online version in colour.)

terms of the number of primate species that consumed them, as well as their proportion across primate diets). Species of both families were consumed by multiple primate species from all major geographic areas, clades and dietary niches, unlike other plant families. Moraceae is among one of the most diverse angiosperm families (ca 1100 species [38]) and is found across a wide variety of habitats. Its fruits and leaves are consumed by a wide variety of primate species, including spider monkeys, chimpanzees, gibbons, howler monkeys, colobus monkeys and gorillas [39–44]. Ficus, the largest genus in Moraceae, is also consistently among the most diverse genera in lowland tropical forests across all three tropical biogeographic realms [45] and may thus explain the large contribution of Moraceae across primate diets (electronic supplementary material, figure S8). Furthermore, young leaves and ripe fruits of Ficus are available throughout the year since individuals tend to be asynchronous in phenology, thus offering constant food supply for primates to meet their basic nutrient needs, including high levels of calcium [46–50], and making them a keystone resource for many frugivores [43,48,51–60]. Overall, the reliability and quality of Fabaceae and Moraceae species as food sources likely explains their prevalence and importance and high-lights their role as keystone families in primate diets globally.
(b) Phylogenetic patterns in the consumption of plant families across primate diets

The degree of consumption of Fabaceae and Moraceae was random with respect to the primate phylogeny, although we detected a weak association between the occurrence of consumption of Fabaceae and the primate phylogeny. The general lack of a phylogenetic signal in family-specific consumption patterns contrasts with the fact that the degree of frugivory or folivory in primates is associated with a broad suite of traits, many of which are strongly constrained by evolutionary history [24]. For example, more frugivorous primates tend to have larger brains compared to more folivorous species [61,62]. Large brain size may be particularly advantageous when exploiting asynchronously fruiting plants such as Ficus [47,48,63,64], which must be tracked at the individual tree level rather than across all individuals of the same species, thus requiring increased demands on spatial and temporal memory [62,65]. By contrast, different primate lineages may possess clade-specific dietary adaptations to deal with the potentially high fibre or toxin content of a leaf-based diet, such as the complex foregut of colobines, enlarged colon for hindgut fermentation in howlers, and specialized teeth of pithecines [66–68]. However, family-level patterns of consumption may not necessarily mirror patterns of folivory/frugivory among primates. Plant families are rarely consumed for a single plant part (e.g. fruit versus leaves), and the degree of consumption of different plant families may be more strongly driven by local or regional differences in the abundance of those plant families than variation in phytochemistry or morphology across plant families.

(c) Determinants of primate body mass and home range size

Our SEM results support the hypothesis that space use by animals increases with larger body mass [69] and that more folivorous primates tend to occupy smaller home ranges than more frugivorous species [13]. This may be explained by the greater absolute nutritional requirements of larger bodied primates and the less patchy distribution of leaves compared to fruits [1,70]. Furthermore, folivores with larger body mass can more easily subsist on a low-quality diet due to lower energy demand per gram of body and increased gut capacity for fermenting fibre [13]. We did not, however, find any effect of the proportion of fabaceous leaves in the leaf diet on either body mass or home range size. This was surprising since fabaceous leaves are generally regarded as high-quality foliage relative to leaves from other families, as well as being widely available in tropical ecosystems [54,55]. Thus, primates that consume fabaceous leaves to a large degree may be expected to have smaller home range requirements or may be able to more efficiently digest them without having to be larger in size. This discrepancy could reflect (i) high variability in the nutritional quality of leaves among Fabaceae species, (ii) that secondary compounds may be counteracting the nutritional benefits or (iii) that high-quality leaves of legumes may be more patchily distributed than expected due to greater competition thus negating any effect of individual plant availability on home range size [71,72].

When analysing patterns of frugivory, we found that primates with a larger percentage of Moraceae in their fruit diet had smaller home range sizes. This may be explained by the greater availability of Moraceae fruits year-round compared to other fruiting tree species [47,48], suggesting this family to be uniquely important as a keystone resource to many primates [43,50,53]. When controlling for phylogeny, however, the positive relationship between folivory and body mass and negative relationship between Moraceae fruit consumption and home range size were no longer statistically significant. This suggests that these trends are primarily driven by certain primate clades (electronic supplementary material, figures S6 and S7). The negative effect of Moraceae consumption on home range size appears to be primarily driven by the cercopithecids.

We acknowledge, however, that any global comparative approach of primate diets is limited by the available information on feeding records and does not usually reflect the nutritional content of the food items consumed. In addition, the quality of the same plant parts will vary within their respective families. A deeper understanding of how morphological and phytochemical variation, as well as the relative abundance, of different plant resources across plant species, genera and families shape the traits of specific primate species will add additional insights into plant–primate evolutionary relationships.

5. Conclusion

Plants from the Moraceae and Fabaceae families form a core component of primate diets worldwide and may potentially be keystone resources for primates. In particular, the consumption of Moraceae may be associated with certain primate traits, such as home range size, which we argue may be due to the year-long reliability of moraceous fruits. We thus show that primates may be intrinsically and subtly shaped by the plants that they consume. The high proportion of fruit in the diet of primates also highlights their importance as crucial seed dispersers for many angiosperm species across ecosystems [2]. Our study also shows that comparative approaches may provide further insights into the role of diet in primate ecology and evolution. We encourage primatologists to continue with field studies on primate diets that report valuable and detailed information on plant dietary items clearly organized by plant species and part to allow for future comparisons across studies (see [4]).

Data accessibility. Full dataset and metadata, phylogeny, and R scripts used to perform data cleaning, analyses and figure generation for this study are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.sbcc2fr40 [73].

The full list of references compiled for our dataset is also available in the electronic supplementary material [74].

Authors’ contributions. J.Y.L.: data curation, formal analysis, funding acquisition, investigation, methodology, resources, software, validation, visualization, writing-original draft; writing-review and editing; M.D.W.: conceptualization, funding acquisition, investigation, project administration, resources, supervision, writing-original draft, writing-review and editing; J.V.: data curation, investigation and writing-original draft; W.D.K.: funding acquisition, investigation, methodology, project administration, resources, supervision, writing-original draft, writing-review and editing.

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