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Human-Induced Downsizing of Animal Communities Weakens Trait Matching Between Tropical Plants and Frugivores

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ABSTRACT

Defaunation of large-bodied animals threatens essential ecosystem functions, such as seed dispersal. However, the consequences of this human-induced downsizing of animal communities for plant-frugivore trait matching—the alignment between frugivory-related plant traits (e.g., fruit size) and frugivore traits (e.g., body mass)—remain unquantified at macroecological scales. Here, we examine how human disturbance and environmental conditions influence trait matching in tropical plant-frugivore networks. We compiled fruit size data for 1927 plant species from primary sources, along with body mass and dietary information for 1120 frugivorous animal species (birds, mammals and reptiles), and integrated these with 12,708 plant-frugivore interactions recorded across 102 networks. Using fourth-corner analyses and structural equation models (SEMs), we quantified how human disturbance and environmental conditions directly and indirectly affected trait matching strength (fruit-size-to-body-mass correlation) across networks. SEMs revealed that human disturbance weakened trait matching by reducing the range of frugivore body masses within networks, whereas wet and productive environments promoted a higher proportion of fruit in frugivore diets, leading to stronger trait matching. Our results demonstrate that human disturbance weakens plant-frugivore trait matching through the downsizing of animal communities, thereby providing a quantitative assessment of the decoupling of coevolved relationships between fruiting plants and their animal seed dispersers.

1 | Introduction

Mutualistic interactions between fruiting plants and frugivorous vertebrates are fundamental to seed dispersal and the maintenance of biodiversity in tropical regions (Howe 1986; Jordano 2000). These interactions form intricate networks of species interdependence, where the survival and reproductive success of both plants and frugivores are closely linked (Bascompte 2009). In tropical rainforests, 70%–94% of woody plant species rely on animals for seed dispersal, while many vertebrates depend on fleshy fruits as essential food resources (Howe 1986; Jordano 2000). A crucial mechanism driving these interactions is size-based trait matching, where large frugivores tend to consume large fruits, whereas small frugivores favour small ones, creating a size-based pattern that shapes the structure of these mutualistic networks (Burns 2013; González-Castro et al. 2015). In birds, size constraints are particularly evident, as species that swallow fruits whole (gulpers) are limited by their gape size, while those that chew fruits (mashers) tend to avoid larger fruits due to their proportionally larger seed size (Rojas et al. 2021; Wheelwright 1985). Although mammals are less restricted by gape size, they still tend to follow size-based consumption patterns, with large-bodied species preferring large fruits (Flörchinger et al. 2010; Muñoz et al. 2019). In communities of both birds and mammals, body mass often serves as a reliable predictor of size-based trait matching (Donatti et al. 2011; Muñoz et al. 2019).

Size-based trait matching is central to endozoochorous seed dispersal interactions and a key determinant of dispersal outcomes (Jordano et al. 2007; Wotton and Kelly 2012). Large vertebrates, in particular, provide unique dispersal services by transporting seeds over long distances due to their extensive home ranges and prolonged gut retention times (Carbone et al. 2005; Fell et al. 2023; Jordano et al. 2007; Wotton and Kelly 2012). Furthermore, size matching plays a crucial role in niche partitioning within plant–frugivore ecological networks. Indeed, body mass and fruit size are instrumental in resource partitioning, allowing frugivores to occupy distinct ecological niches based on the size of the fruits they consume (Todeschini et al. 2020). This niche partitioning reduces direct competition, promotes species coexistence and supports high biodiversity in tropical ecosystems (Fleming 1979; Sterck et al. 2011). As a result, plant–frugivore networks characterised by a wide range of fruit sizes and frugivore body masses can maintain more ecological niches, enabling species to specialise in different resources (Flörchinger et al. 2010; Todeschini et al. 2020). This broader niche availability encourages functional specialisation, which is often reflected in morphological trait matching relationships between plants and frugivores (Bender et al. 2018; Dehling et al. 2014). Consequently, networks with greater variation in fruit sizes and frugivore body masses may exhibit stronger patterns of morphological trait matching.

Human activities, such as deforestation and poaching, are driving widespread defaunation—the decline or loss of animal species from ecological communities—at alarming rates (Harrison et al. 2016; Lewis et al. 2015; Wright et al. 2007). These pressures have led to substantial population declines and extinctions of many large-bodied animals across tropical forests, including keystone frugivorous vertebrates (Harrison et al. 2016; Lewis et al. 2015; Wright et al. 2007). This selective loss of large-bodied animals, a phenomenon known as downsizing, disrupts critical ecological processes and weakens both the structural and functional integrity of seed dispersal networks (Donoso et al. 2020; Pérez-Méndez et al. 2015). Notably, downsizing tends to reduce functional robustness—such as long-distance seed dispersal and seed germination success—more rapidly than structural robustness (Campagnoli et al. 2025; Donoso et al. 2020). Although the consequences of downsizing for seed dispersal and plant recruitment are increasingly recognised (Markl et al. 2012; Pérez-Méndez et al. 2015), its effects on trait matching between plants and frugivores remain poorly understood. Downsizing is expected to weaken trait matching strength in plant–frugivore networks, as illustrated in Figure 1, where intact networks maintain strong alignment between plant fruit size and frugivore body mass, whereas downsized networks exhibit weaker alignment due to the loss of large-bodied dispersers.

At macroecological scales, where environmental factors and biogeographic processes gain importance, trait matching may also be shaped by how these conditions have influenced the occurrence of frugivory-related plant and animal traits (Cabral et al. 2025; Lim et al. 2020; McFadden et al. 2022; Wölke et al. 2023). For example, warmer and wetter climates, along with factors such as actual evapotranspiration (AET) and net primary productivity (NPP), have been linked to the evolution of endozoochorous fruits and are positively associated with the species and functional richness of plants and frugivores (Cabral et al. 2025; Kissling et al. 2009; Vasconcelos et al. 2023). NPP, a key indicator of food availability in terrestrial ecosystems, is associated with plant species richness and plant traits, favouring large plants with large seeds that are adapted to germinate in low-light conditions in the understory (Moles et al. 2007; Waide et al. 1999). Taken together, these factors—providing high resource availability—constitute benign environmental conditions that support diverse plant and frugivore communities. Furthermore, greater availability of plants with edible fruits supports higher abundance and diversity of frugivores, promoting a greater degree of frugivory among both birds and mammals (Cavalcante et al. 2021; Fleming 2005; González-Varo et al. 2022; Kissling et al. 2007). Frugivores that heavily rely on fruit in their diet have been observed to show greater selectivity and may tend to choose fruits based on specific morphological and chemical traits, such as seed size and nutritional content (Malanotte et al. 2019). In contrast, opportunistic frugivores appear to be less selective and are likely to consume fruits according to availability and as a dietary supplement (Malanotte et al. 2019). This distinction suggests that frugivores with a higher dependency on fruit in their diet could engage in more size-matched interactions with plant fruits. While it is evident that environmental conditions influence local frugivory levels and that frugivory may be linked to trait preferences and potentially size-matching, it remains unclear how the degree of frugivory within a plant–frugivore network affects the strength of trait matching.

In this study, we integrated data on plant and animal traits with an extensive global dataset of seed dispersal interactions to assess how human disturbance and environmental conditions both directly and indirectly affect trait matching in plant–frugivore networks across the tropics. Previous work has demonstrated that trait matching varies globally across plant–frugivore networks, and that latitude (e.g., seasonality), islands and biogeography explain part of this variation (Huang et al. 2025; McFadden et al. 2022; Morán-López et al. 2025). However, these studies have only considered interactions with birds. Furthermore, the importance of human disturbance and (Quaternary) defaunation on plant traits (e.g., fruit or seed size) or size-matching has been shown for specific groups (e.g., palms, Lim et al. 2020) or regions (e.g., Madagascar, Pu et al. 2025; Andes, Dehling et al. 2014), but these studies often rely on co-occurrence rather than observed interactions (but see Dehling et al. 2014), or focused on the consequences of defaunation using simulations (Donoso et al. 2017). Importantly, it remains a challenge to comprehensively assemble data on dispersal units across many plant

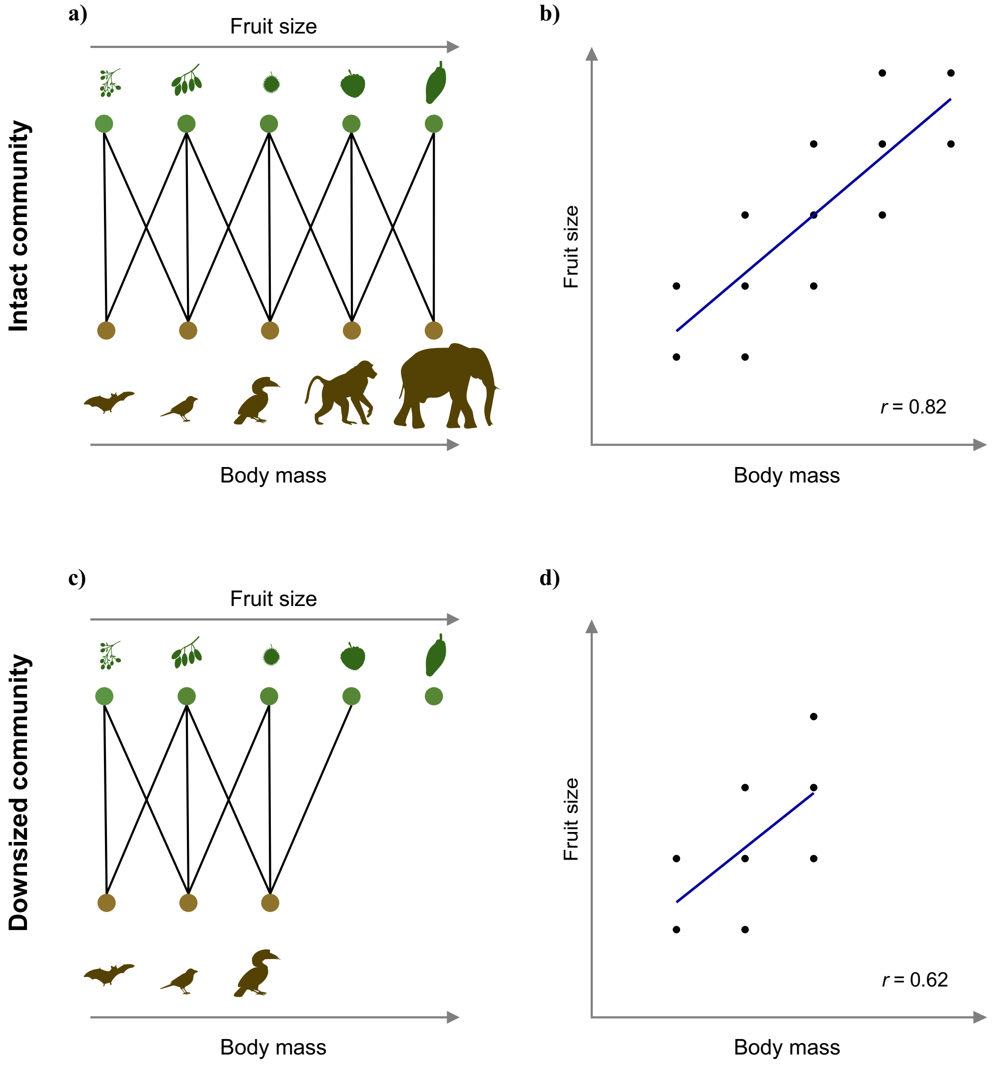

FIGURE 1 | Conceptual diagram of fruit-size-to-body-mass trait matching in intact and downsized plant–frugivore networks. (a) Plant–frugivore network representing an intact community, characterised by a broad range of plant fruit sizes and frugivore body masses. (b) Trait matching in the intact community, shown as a strong positive Pearson correlation between plant fruit size and frugivore body mass. (c) Plant–frugivore network representing a downsized community, where large-bodied frugivores are absent, reducing the range of frugivore body masses, while the range of fruit sizes remains unchanged. (d) Trait matching in the downsized community, reflected by a weaker Pearson correlation, indicating reduced alignment between plant fruit size and frugivore body mass due to the loss of large-bodied dispersers. For illustrative purposes, regression lines are shown in (b) and (d) in blue.

species and identify the limiting size dimension for dispersal (e.g., seed or fruit size).

Here, we address these knowledge gaps by assembling new plant trait data from primary sources, rather than relying on imputed values, by including all observed interactions among plants and vertebrates, and by quantifying the direct and indirect pathways by which human disturbance and environment affect trait matching. First, we hypothesise (H_1) that the strength of fruit-size-to-body-mass trait matching varies across ecological networks due to variation in ecological and biogeographical context. Hence, we expect spatial (biogeographical) structuring in trait matching across networks. Second, we hypothesise (H_2) that human disturbance leads to the downsizing of animal communities (i.e., loss of large-bodied species), thereby decreasing the range of frugivore body masses within a network. Consequently, this may reduce the strength of the fruit-size-to-body-mass trait matching (Figure 1). Third, we hypothesise (H_3) that benign environmental conditions influence the average degree of frugivory within a network, which in turn affects the strength of the fruit-size-to-body-mass trait matching. Specifically, we expect that networks in warmer, wetter and more productive environments, with higher rates of evapotranspiration, will support a greater proportion of animals with a high proportion of fruit in their diet, leading to greater selectivity and size-based interactions and hence stronger trait matching.

Our findings demonstrate that human pressures disrupt trait-based interaction patterns across broad spatial scales. As trait matching is a key determinant of seed dispersal outcomes (i.e., both the quality and quantity of dispersal events), its breakdown—particularly through the loss of large-bodied frugivores—can compromise essential functions such as long-distance dispersal and the movement of large seeds

(Albert-Daviaud et al. 2020; Donoso et al. 2020). This erosion of functional complementarity between plants and frugivores in mutualistic networks threatens the resilience of tropical communities by reducing their capacity to recover from disturbance (Campagnoli et al. 2025; Pérez-Méndez et al. 2015). These results underscore the practical importance of conserving functional diversity—particularly the roles of large-bodied frugivores—but also advance ecological theory by demonstrating how trait matching structures mutualistic networks and how these interaction patterns are altered by variation in human disturbance and environmental conditions across macroecological scales.

2 | Materials and Methods

2.1 | Plant–Frugivore Network Data

We sourced the plant–frugivore interaction data from a comprehensive global dataset compiled by Fricke and Svenning (2020). This dataset comprises 410 local interaction networks, each constructed based on direct observations of animals interacting with fruits or seeds or from seeds retrieved from captured animals. These networks are bipartite, representing interactions between animal and plant species. While some networks recorded interaction frequencies, we used them in a binary format (presence or absence) due to inconsistencies in how frequencies were recorded across the dataset. This study focused on a subset of networks from tropical regions, defined geographically as the area between the Tropic of Cancer and the Tropic of Capricorn. This focus was chosen due to the importance of frugivory and seed dispersal mutualisms in the tropics, as well as the dependence of woody plants on frugivores for seed dispersal (Jordano 2000). The initial subset contained 251 spatially and temporally distinct tropical interaction networks (see Dataset S1). To account for repeated sampling at the same location over time, we aggregated unique plant–frugivore interactions from networks with the same coordinates into single composite networks, resulting in a final dataset of 181 geographically distinct networks ($n = 145$ non-composite networks; $n = 36$ composite networks formed by merging 2–11 original networks, mean ± SD: 2.94 ± 1.67). Prior to data analysis, the nomenclature of animal and plant species was updated to reflect taxonomic revisions made since the compilation of the original dataset. Animal species names were standardised following HBW and BirdLife International (2021) for birds, the International Union for Conservation of Nature (IUCN 2022) for mammals, and Oskyrko et al. (2024) for reptiles. Plant species names were standardised using the World Checklist of Vascular Plants (WCVP) with the accompanying 'rWCVP' R package (Brown et al. 2023; Govaerts et al. 2021). All data processing steps and analyses were conducted in R v4.4.1 and RStudio (R Core Team 2024).

2.2 | Plant Functional Trait Data

We compiled data on frugivory-related plant traits, including fruit and seed dimensions (length and width), fruit type (e.g., berry, drupe, capsule; see Dataset S2), dehiscence (presence or absence) and seed fleshy appendages (presence or absence) for all 2406 plant species that were present in the 181 ecological networks (see supplementary methods in Text S1 for details). Trait data were complete for 94.4% of the species ($n = 2272$) and were primarily sourced from floras and monographs (79%), supplemented by scientific articles (19%) and photographs (2%) (see Dataset S2 for data and sources). Plant trait data were preferred under the accepted species name; however, when unavailable, they were retrieved from taxonomical homotypic synonyms following the WCVP. Methods for measuring fruit size vary considerably across studies. Some approaches consider fruit length or width, while others use a composite measure that sums fruit length and width. Both approaches present limitations: fruit length or width may not always correspond to the fruit's longest or shortest axis, and combining length and width into a single metric may fail to capture the constraints frugivores face during fruit consumption. To address these inconsistencies, we defined fruit size as the smallest reported axis of the dispersal unit (either fruit or seed), as this dimension is most likely to represent the key constraint for frugivores during ingestion. For indehiscent fruits, frugivores generally interact with the entire fruit, as the fleshy pericarp remains intact. In contrast, for dehiscent fruits, frugivores often interact with the seeds rather than the usually dry pericarp, especially when fleshy structures such as arils, sarcotestae, or elaiosomes are present. Accordingly, for the trait matching analyses, we selected the smallest axis of the dispersal unit, whether it was fruit length or width for indehiscent fruits or seed length or width for dehiscent fruits. Throughout the study, we refer to this measurement as 'fruit size'.

2.3 | Frugivore Functional Trait Data

We compiled data on frugivory-related animal traits, including body mass, degree of frugivory (percentage of the diet composed of fruit), degree of granivory (percentage of the diet composed of seeds), beak dimensions and gape size for all 1226 animal species that were present in the 181 ecological networks. Trait data were complete for 98.9% of the species ($n = 1213$) and were primarily sourced from established databases: AVONET (Tobias et al. 2022), COMBINE (Soria et al. 2021), EltonTraits (Wilman et al. 2014), ReptTraits (Oskyrko et al. 2024) and McFadden et al. (2022) (see Dataset S3 for data and sources). Animal trait data were preferred under the accepted species name; however, when unavailable, they were retrieved from taxonomic synonyms, following HBW and BirdLife International (2021) for birds and Soria et al. (2021) for mammals. In cases of discrepancies between accepted names and synonyms, the mean trait values were used. Dietary information was available for 1102 species, with species-specific data for 93.7% of them; for the remaining 6.3%, diet was imputed using genus or family-level information (see Wilman et al. 2014 for details). We selected body mass as the primary trait because it provides a comparable metric across birds, mammals and reptiles. While bird-specific traits such as beak volume and gape size are often used in trait matching studies, body mass (as a proxy of body size) was chosen for its broader applicability across taxa. This decision was supported by the strong correlations observed between body mass and beak volume ($r = 0.81$) and gape size ($r = 0.85$) in birds. The final dataset was composed predominantly of birds (75.8%), followed by mammals (23.3%) and reptiles (0.8%), reflecting the overall importance of these guilds for frugivory in the tropics (Fleming and Kress 2013). Nonetheless, the relative representation of these taxonomic groups may vary across regions in response to differences in climate, ecological conditions and biogeographic context.

2.4 | Human Disturbance and Environmental Data

Human disturbance and environmental data were assembled and extracted for each plant–frugivore network at spatial resolutions of 1 and 5 km using ArcGIS Pro 3.3 (Esri 2024). Human disturbance data were derived from the Global Human Modification (gHM) dataset (Kennedy et al. 2020), which provides an integrated (i.e., cumulative) measure of human alteration of terrestrial landscapes at 1 km resolution. This continuous metric (ranging from 0 to 1) represents the proportion of land modified by human activities and integrates 13 indicators of disturbance, including human population density, built-up areas, cropland, livestock, major roads, minor roads, two-track roads, railroads, mining, oil wells, wind turbines, powerlines and night-time lights, based on spatially explicit global datasets with a median reference year of 2016 (Kennedy et al. 2020). Environmental data were sourced from CHELSA V2.1 (Karger et al. 2017), which provided annual temperature (°C), precipitation (mm), and NPP (g C/m^2) at a 1 km resolution, averaged over the period 1981–2010. Although precipitation and NPP showed a strong correlation (r=0.71), this remained below the commonly accepted multicollinearity threshold of r=0.80 (Field et al. 2012). Consequently, both variables were retained, as their influence on frugivory may act through distinct ecological mechanisms. Additionally, AET (mm) (Elnashar et al. 2021) was extracted as the annual average across the period 1982–2019 at a 1 km resolution. All network-level data are provided in Dataset S4.

2.5 | Trait Matching Using Fourth-Corner Analysis

To investigate the strength of trait matching between plant fruit size and frugivore body mass, we conducted fourth-corner analyses based on the methodology outlined by Dehling et al. (2014). The fourth-corner analysis integrates three matrices: the plant trait matrix (R), which consists of plant species and their associated traits; the animal trait matrix (Q), which consists of animal species and their traits; and the interaction matrix (L), which records species interactions (presence or absence of interactions between plant and animal species). From these, the analysis calculates a fourth matrix (X), which quantifies the relationship between plant and animal traits by computing coefficients for each trait pair. In this case, the analysis calculates a Pearson correlation coefficient (r) to measure the relationship between fruit size and body mass of interacting partners. To test the null hypothesis (i.e., no correlation between plant and animal traits, X=0), we employed a null model approach, which randomised the plant and animal identities in the interaction matrix (L) through permutation testing (ter Braak et al. 2012; Dray and Legendre 2008). This permutation approach, known as model type 6 (implemented using the *fourthcorner* function in the 'ade4' R package), combines the outcomes of two permutation models: model type 2 (where plant species are permuted) and model type 4 (where animal species are permuted) (Dray and Dufour 2007). The final p-value is determined by selecting the higher of the two p-values from these permutations. We specifically chose model type 6 because previous models (types 1–5) exhibit inflated Type I error rates (Dray and Legendre 2008).

The fourth-corner analyses were conducted at three distinct levels, considering only interactions between plant and animal species for which both fruit size and body mass data were available. First, we assessed trait matching across all unique species interactions between plants and frugivores in the dataset (n=12,850 unique interactions between n=2240 plant species and n=1204 animal species). Second, we examined trait matching at the dietary level, using the average fruit size consumed per unique animal species (n=833 unique animal species that had interactions with at least three unique plant species). We focused on the average instead of maximum fruit size because not all recorded interactions involved endozoochory, and in some cases, the animal species were smaller than the fruits and seeds with which they interacted, indicating that seeds could not have been ingested. To support this decision, we compared linear regressions between average fruit size consumed and frugivore body mass compared to maximum fruit size consumed and frugivore body mass, where the former showed a better fit (as reflected by a higher R^2; see Figure S1). Third, we evaluated trait matching within individual ecological networks, focusing on unique species interactions between plants and frugivores within each network.

To develop a robust measure of trait matching strength per network suitable for downstream analyses, we restricted the analysis to networks containing at least 30 interactions involving a minimum of four plant and four animal species (n=102 networks, including n=12,708 interactions between n=1927 plant and n=1120 animal species). These thresholds were set to ensure adequate variation in both fruit size and frugivore body mass and to prevent statistical biases associated with small sample sizes, which can distort Pearson's correlation coefficients (Aggarwal and Ranganathan 2016; Fraenkel et al. 2012). Furthermore, networks varied considerably in sampling effort and method (e.g., focal observations, faecal sampling, camera trapping), although the precise extent of this variation is unknown (Fricke and Svenning 2020). Networks with fewer recorded interactions (closer to 30) are likely to be undersampled compared to those with a higher number of interactions (closer to 600). Notably, the (remaining) composite (i.e., spatially aggregated) networks contained more interactions (mean ± SD: 166 ± 128, n=19) than non-composite networks (mean ± SD: 115 ± 125, n=83), reflecting increased sampling effort at those sites. To account for this variation, we implemented a weighting scheme for the trait matching correlation coefficients, assigning greater weight to networks with more interactions while reducing the influence of networks with fewer interactions. This was achieved by conducting a meta-analysis, beginning with Fisher's z-transformation of Pearson's correlation coefficients (r) to normalise their distribution, following standard procedures (using the *escalc* function in the 'metafor' R package; Viechtbauer 2010). The square root of the total number of interactions recorded per network was used as a proxy for sample size, following Bender et al. 2018, to ensure that networks with more interactions were appropriately weighted. The meta-analysis was performed using a random-effects model, with each network weighted by the inverse variance of its correlation coefficient. This approach ensured that networks with lower variance (i.e., larger sample sizes) were given greater weight, while those with higher variance (i.e., smaller sample sizes) were down-weighted. This approach increases the reliability of the z-transformed Pearson's r values in

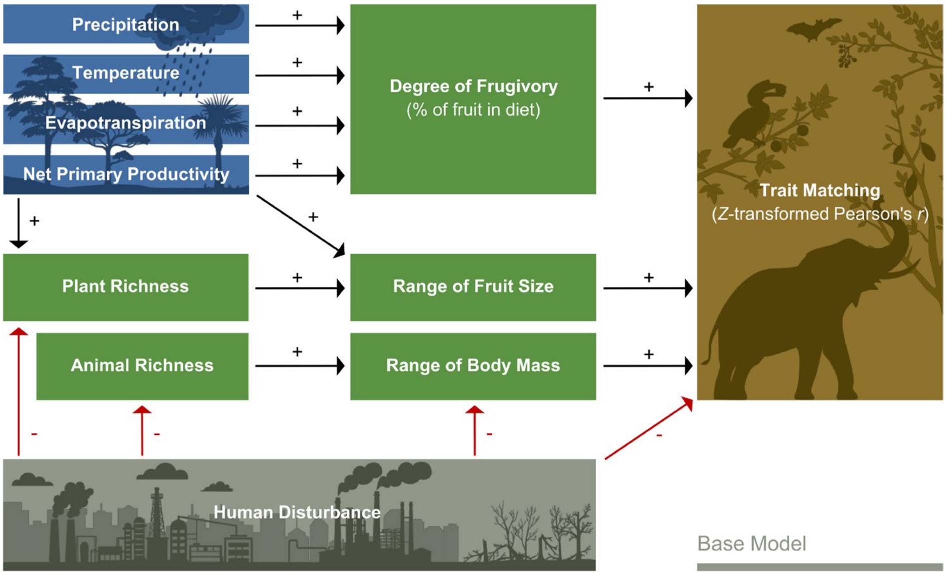

FIGURE 2 | Hypothesised predictors of trait matching in plant–frugivore networks. The structural equation model (SEM) shows the direct and indirect effects of environmental conditions (blue) and human disturbance (grey) on plant and animal characteristics (green) and plant–frugivore trait matching across tropical networks (brown). Arrows indicate the predicted causal relationships, with the signs and colours of the arrows reflecting whether the effects are expected to be positive (black) or negative (red).

relation to sample size, as larger networks provide more robust estimates of trait matching. Following the meta-analysis, we extracted the weighted *z*-transformed Pearson's *r* values for each network, which were then used in subsequent analyses to represent trait matching strength at the network level. To evaluate the impact of different network sampling methods on our trait matching coefficients and findings, we compared trait matching strength between networks that used different sampling methods using a Kruskal–Wallis test.

2.6 | Biogeographical Structure in Trait Matching

To evaluate biogeographical structure (H_1) in trait matching, we mapped the strength of trait matching for each plant–frugivore network on a global map and visually inspected spatial correlation. Furthermore, we categorised networks into zoogeographic realms based on the classification system from Holt et al. (2013). Four realms had sufficient sample sizes for analysis: 'Panamanian', 'Neotropical', 'Afrotropical' and 'Oriental', including a total of $n = 90$ networks. A Kruskal–Wallis test was performed to determine whether these regions differed significantly in trait matching strength.

2.7 | Human Disturbance and Environmental Effects on Trait Matching Using Structural Equation Models

To assess the impact of human disturbance (H_2) and environmental conditions (H_3) on the variation in trait matching strength across networks, we employed structural equation models (SEMs). Specifically, we evaluated the direct and indirect effects of human disturbance, environmental conditions (temperature, precipitation, NPP and AET), functional traits (range of fruit size, range of body mass and average degree of frugivory) and plant and animal species richness on the strength of trait matching across ecological networks (Figure 2). Because our dataset is restricted to tropical regions, variation in temperature and precipitation seasonality is relatively limited. Nevertheless, we tested whether these climatic variables influenced the average degree of frugivory across networks but detected no significant effects. The range of fruit size and body mass within each network was quantified as the difference between the logarithms of their maximum and minimum values [log(max)−log(min)]. Plant and animal species richness were included to account for sampling effects, as communities with higher richness may be more likely to exhibit extreme trait values. We also hypothesised a direct negative impact of human disturbance on plant richness and animal richness, as supported by previous studies (Clark and Covey 2012; Kirika et al. 2008). Given the variation in sampling effort across networks, species richness estimates could be influenced by the number of recorded interactions. To control for this, we used a proxy for plant and animal species richness, calculated as the observed richness divided by the total number of recorded interactions per network. This ratio was square root-transformed to approximate normality and used as a standardised measure of species richness per interaction in the SEMs. Moreover, the average degree of frugivory per network was calculated based on dietary information for the interacting animal species (i.e., % fruit in diet) and averaged from all interactions across each network. Across networks, the range was 11.81%–100% (SD: 25.84%). We log-transformed the average degree of frugivory to normalise its distribution. To evaluate model assumptions, we used the 'performance' package in R (Lüdecke et al. 2021) to test for normality, heteroscedasticity and multicollinearity across regression paths. While most regression paths satisfied these assumptions, deviations from normality were observed in the paths involving the range of body mass and trait matching. Hence, we applied a maximum likelihood estimator with robust standard errors (MLR), which adjusts for non-normality and provides more reliable and accurate standard errors and model fit indices (Li 2021).

We initiated the modelling process by constructing an a priori SEM that incorporated all hypothesised relationships between exogenous and endogenous variables (Figure 2). From this initial model, we systematically removed non-significant paths ($p > 0.05$) until the final model contained only statistically significant pathways ($p < 0.05$). To evaluate model fit, we ensured the model was over-identified (df > 0) and assessed its performance using several fit indices: the scaled chi-square test ($p > 0.05$), robust comparative fit index (CFI > 0.95), robust Tucker–Lewis index (TLI > 0.95) and robust root mean square error of approximation (RMSEA < 0.08) (Grace et al. 2012; Li 2021; Streiner 2006; West et al. 2023). Once a model with only significant paths and an acceptable model fit was achieved, we extracted the standardised path coefficients. All SEM analyses were performed using the 'lavaan' package in R (Rosseel 2012). Figures were created using the 'ggplot2' and 'patchwork' R packages (Pedersen 2024; Wickham et al. 2024). Figures were subsequently exported and edited in Inkscape (Inkscape 2025).

2.8 | Sensitivity Analyses of the Structural Equation Model

To assess the robustness of the relationships (effect sizes and significance) identified in the main SEM and to examine sources of uncertainty, we conducted a series of sensitivity analyses addressing temporal, spatial, ecological and methodological considerations. First, we evaluated how the temporal mismatch between the human disturbance data—derived from an integrated human modification index with a median reference year of 2016 (Kennedy et al. 2020)—and the plant–frugivore interaction data—which spanned a broader temporal range from 1961 to 2017 with a median sampling year of 2005—affected the SEM results. This mismatch raised concerns about whether the human disturbance data accurately reflected conditions during the periods when the interactions were recorded. To address this, we repeated the SEM using only networks sampled since 2000 ($n = 63$ networks), representing a 38% reduction in sample size relative to the main analysis. In addition to temporal sensitivity, we examined the impact of spatial resolution. The main analysis used environmental and human disturbance variables extracted within a 1 km buffer around each network; however, some networks may have imprecise geographical coordinates (see Fricke and Svenning 2020). We therefore repeated the SEM using environmental and human disturbance data extracted with a 5 km buffer (for all $n = 102$ networks) to test whether a broader spatial grain affected the observed relationships between trait matching and environmental conditions or human disturbance. Beyond temporal and spatial considerations, we also addressed the assumption that recorded interactions reflect mutualistic (seed dispersal) rather than antagonistic (seed predation) interactions. To focus on interactions more likely to result in seed dispersal, we repeated the SEM using only interactions with animals whose degree of frugivory (% fruit-eating) was equal to or greater than their degree of granivory (% seed-eating), producing a dataset that is more likely to reflect effective dispersal events. Finally, to evaluate the potential influence of our weighting scheme on trait matching estimates, we conducted the analysis without weighing Fisher's z-transformed Pearson's r values by sample size, allowing us to assess whether the weighting scheme affected our conclusions.

3 | Results

3.1 | Plant–Frugivore Network Data Overview

We analysed a subset of the plant–frugivore interaction data retrieved from Fricke and Svenning (2020), which consisted of 102 spatially distinct tropical plant–frugivore networks, comprising 12,708 interactions, of which 11,607 were unique (due to the recurrence of certain plant–frugivore interactions across the networks). These networks included 146 plant families, 1927 plant species, 113 animal families and 1120 animal species. On average, each network contained 28 plant species and 23 animal species. The number of interactions per network ranged from 30 to 671, with a mean of 125 interactions (SD: 126). Fruit sizes ranged from 1 to 250 mm, while frugivore body masses varied from 5.6 g to 4750 kg. Notably, the dataset included both the largest tree-borne fruit in the world, jackfruit (*Artocarpus heterophyllus*), and the largest terrestrial mammal, the African bush elephant (*Loxodonta africana*).

3.2 | Trait Matching Across Tropical Networks

Fourth-corner analyses revealed significant trait matching between plant and frugivore traits, with positive relationships observed between fruit size and body mass across unique species interactions (Figure 3a), the average fruit size consumed per frugivore species (Figure 3b), and at the plant–frugivore network level (Figure 3c). At the level of unique species interactions, we detected a moderate positive correlation between fruit size and body mass ($r = 0.41$, $p < 0.001$, $n = 12{,}850$) (Figure 3a), which increased when examining the average fruit size consumed per frugivore species ($r = 0.62$, $p < 0.001$, $n = 833$) (Figure 3b). A meta-analysis across plant–frugivore networks demonstrated a significant positive correlation between fruit size and body mass at the network level (random-effects model; Fisher's $z = 0.16$, 95% CI [0.09, 0.23], $p < 0.001$, $n = 102$ networks). These results suggest a general pattern of trait matching between plant fruit size and frugivore body mass across tropical networks. However, fourth-corner analyses at the network level revealed considerable variability (Figure 3c): while some networks exhibited strong positive correlations, others showed weak or even negative associations, highlighting the heterogeneity of trait matching across tropical networks. This variation does not appear to be driven by biogeographical context, as a Kruskal–Wallis test (χ^2-test $= 1.26$, df $= 3$, $p = 0.739$) revealed no significant differences in trait matching across biogeographical realms (Figure S2).

3.3 | Human Disturbance and Environmental Conditions Indirectly Impact Trait Matching

The SEM explained 40% of the variance in plant–frugivore trait matching across tropical networks, with satisfactory robust model fit statistics (scaled χ^2-test $= 0.06$, df $= 20$, robust CFI $= 0.98$, robust TLI $= 0.96$ and robust RMSEA $= 0.07$). The

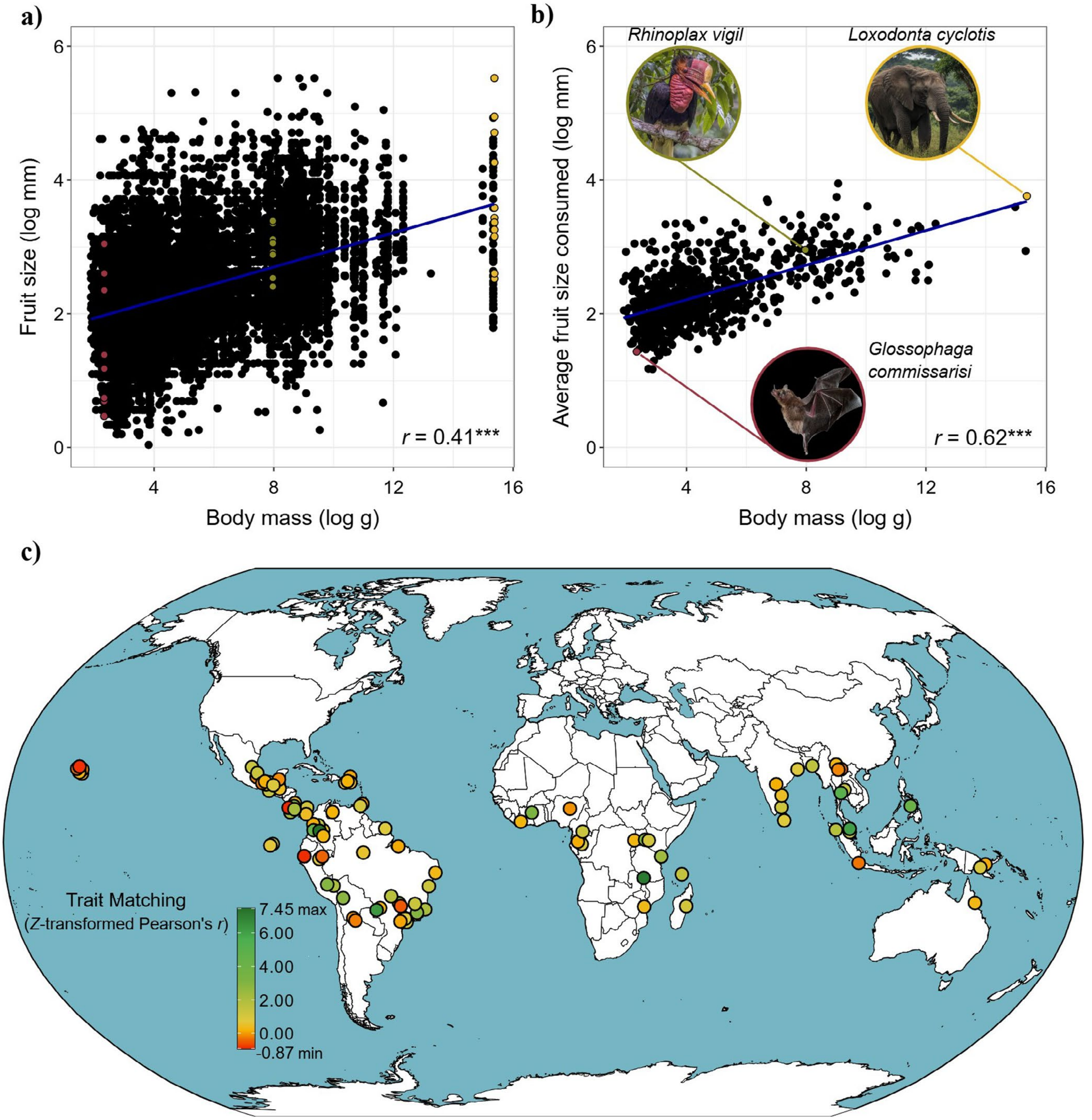

FIGURE 3 | Fruit-size-to-body-mass trait matching in plant–frugivore networks across the tropics. Fourth-corner analyses show trait matching between log-transformed plant fruit size and log-transformed frugivore body mass at various levels of specificity: (a) Trait matching based on species interactions between plants and frugivores ($n = 12{,}850$ unique interactions between $n = 2240$ plant species and $n = 1204$ animal species); (b) Trait matching based on the average fruit size consumed by animal species ($n = 833$ unique animal species that had interactions with at least three unique plant species); (c) Trait matching based on unique species interactions within individual plant–frugivore networks ($n = 102$ networks, including $n = 12{,}708$ interactions between $n = 1927$ plant and $n = 1120$ animal species), represented by weighted Fisher's z-transformed Pearson's correlation coefficients (r) and mapped globally based on the network locality. Significance thresholds were set at: $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. Colours in (a) and (b) indicate animal species with low (purple), medium (green) and large (orange) body masses, and for illustrative purposes, a regression line is shown in blue.

analysis revealed that human disturbance indirectly influenced trait matching by reducing the range of frugivore body masses within networks. Specifically, increased human disturbance may have led to size-selective defaunation, whereby the loss of large-bodied frugivores reduced the range of body masses within networks (standardised path coefficient [std. coeff.] = −0.32; Figure 4), which in turn weakened the strength of trait matching (std. coeff. = 0.58; Figure 4). Although a positive effect of human disturbance on animal richness was detected (std. coeff. = 0.26; Figure 4), the sensitivity analysis restricted to networks sampled

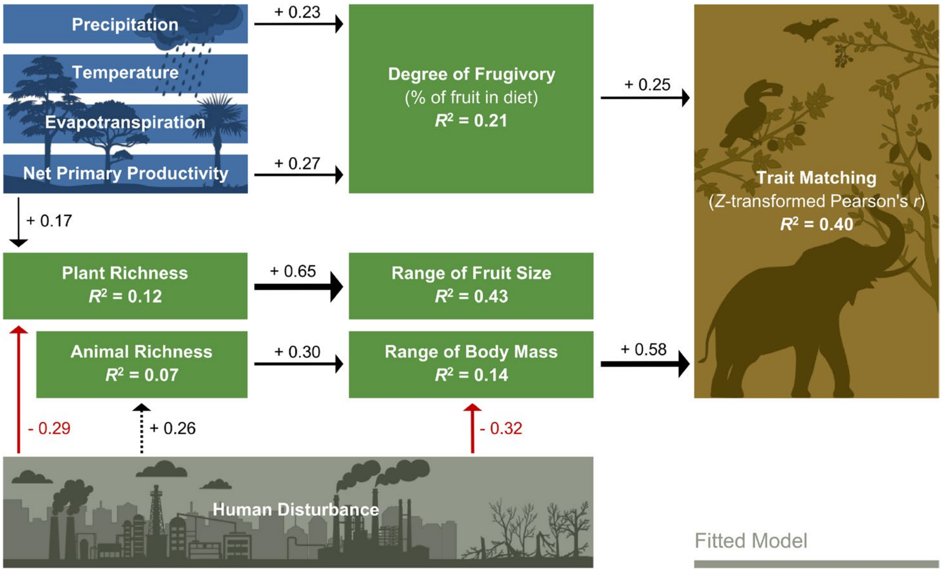

FIGURE 4 | The direct and indirect drivers of fruit-size-to-body-mass trait matching across plant–frugivore networks in the tropics. Structural equation model (SEM) showing the direct and indirect effects of environmental conditions (blue) and human disturbance (grey) on plant and animal characteristics (green) and plant–frugivore trait matching across tropical networks (brown). The strength of trait matching between plant fruit size and frugivore body mass is quantified using Fisher's z-transformed Pearson's r, which is derived from a fourth-corner analysis and weighted by network sample size (square root of interaction count). This analysis includes only ecological networks with a minimum of 30 interactions and at least four plant and four animal species ($n = 102$ networks). Arrows represent standardised effect sizes, with arrow directions reflecting the direction of the effect. Arrow thickness is proportional to the magnitude of the standardised effect size. Arrow colours reflect positive (black) or negative (red) effects. Only statistically significant paths ($p < 0.05$) are shown (see Figure 2 for all tested relationships). R^2 represents the proportion of variance in the response variable explained by the explanatory variables combined. The dashed arrow denotes the effect of human disturbance on animal richness, which becomes statistically non-significant following the sensitivity analysis (see Figure S3).

since 2000 ($n = 63$ networks), given the median sampling year of 2016 for the human disturbance data, revealed that this effect was not statistically robust (see Figures 4, S3), likely reflecting temporal resolution issues rather than an ecological mechanism. Environmental conditions influenced trait matching indirectly through their effect on the average degree of frugivory within networks. Specifically, higher levels of annual precipitation and NPP increased the average degree of frugivory (std. coeff. = 0.23 and 0.27, respectively; Figure 4), which in turn increased trait matching strength (std. coeff. = 0.25). These findings suggest that wetter and more productive environments tend to support networks with a higher proportion of frugivores that depend heavily on fruit in their diets. Additionally, NPP had a positive effect on plant richness (std. coeff. = 0.17), whereas human disturbance had a negative effect (std. coeff. = −0.29). While plant richness increased the range of fruit sizes within networks (std. coeff. = 0.65), variation in fruit sizes did not significantly affect trait matching. Finally, sensitivity analyses—using human disturbance and environmental data within a 5 km buffer (instead of 1 km), restricting the dataset to animal species whose degree of frugivory was equal to or greater than their degree of granivory, and without using the weighting scheme on the trait matching estimates—produced comparable standardised effect sizes and significance levels (see Figures 4, S4–S6 and Table S1), emphasising the robustness of the results. Furthermore, we found no significant differences in trait matching estimates across network sampling methods (χ^2-test = 10.60, df = 5, $p = 0.060$), providing confidence that variation in sampling method did not systematically bias our conclusions (Figure S7).

4 | Discussion

Our findings reveal that trait matching is a prevalent feature of tropical plant–frugivore networks at a global scale, with a consistent alignment between plant fruit size and frugivore body mass across a wide range of plant and animal lineages (Figure 3). However, we also detected substantial variability in trait matching strength (fruit-size-to-body-mass correlation) across networks, without any clear spatial (biogeographical) structure (Figure 3c), thereby rejecting H_1. This variability raises the question of why some networks exhibit stronger trait matching than others. Our study revealed that human disturbance and environmental conditions have a significant impact on trait matching strength through indirect pathways (Figure 4). Specifically, we found that human disturbance reduces trait matching by decreasing the range of animal body masses in plant–frugivore communities, potentially through the defaunation of larger-bodied frugivores, supporting H_2. Additionally, two environmental variables—precipitation and NPP—increased trait matching by promoting higher levels of frugivory within networks, supporting H_3. This study is one of the first to estimate trait matching at a global scale, spanning the Neotropics, Afrotropics and Tropical Asia, using recorded seed dispersal interactions across 102 plant–frugivore networks. Hence, our approach moves beyond the conventional reliance on species co-occurrence data, which assumes that plants and animals with corresponding functional traits interact (e.g., Cabral et al. 2025; Lim et al. 2020; McFadden et al. 2022; Wölke et al. 2023). In addition, this study moves beyond taxa-specific trait matching analyses—such as those focused solely on palms (Arecaceae) (Lim et al. 2020; McFadden et al. 2022; Wölke et al. 2023) or avian frugivores (Huang et al. 2025; McFadden et al. 2022; Morán-López et al. 2025; Zhang et al. 2025)—by adopting a community-wide approach of plants and their interacting avian, mammalian and reptilian frugivores.

4.1 | Human Disturbance Decreases the Strength of Plant–Frugivore Trait Matching Through Downsizing

Our results strongly support the hypothesis that the downsizing of animal communities mediates the effect of human disturbance on plant–frugivore trait matching. Specifically, human disturbance significantly reduced the range of body masses within frugivore communities, whereas networks comprising a larger range of body masses had higher trait matching strength. These results reinforce the view that human-induced defaunation, which disproportionately affects large-bodied animals, is a key driver of the observed mismatches across ecological networks (Galetti and Dirzo 2013; Hansen and Galetti 2009; Pérez-Méndez et al. 2015; Vidal et al. 2014). The Global Human Modification (gHM) dataset, which we used to represent human disturbance, incorporates five stressors and 13 indicators, making it challenging to isolate the individual impacts of each stressor on trait matching (Markl et al. 2012). Furthermore, two key drivers of animal community downsizing, deforestation and poaching (e.g., trophy hunting), which disproportionately target large-bodied animals (Gutiérrez-Granados and Dirzo 2021; Scabin and Peres 2021), are missing. The clandestine nature of these activities complicates global data collection and limits spatial resolution, precluding their inclusion in our analysis. Nevertheless, deforestation is approximated by measurements of livestock, cropland and mining, and the results of the SEM indicate that human presence is associated with the reduction of body mass ranges in networks. This suggests that the selected measure can capture the influence of human activities on the defaunation of large-bodied animals in tropical forests, even though its impact is probably underestimated.

Our findings further support the idea that a human-induced reduction in trait matching strength is driven by small animals consuming relatively large fruits. Large-fruited plant species, having lost their primary large-bodied dispersers, are increasingly reliant on smaller, surrogate dispersers, and these smaller frugivores compensate for the seed dispersal roles typically performed by larger frugivores (Coutant et al. 2022; Cui et al. 2023; Culot et al. 2017; Jansen et al. 2012). However, this may result in reduced seed dispersal effectiveness (Galetti et al. 2013; Guimarães et al. 2008), the breakdown of long-distance dispersal services, or (local) extinction of plant species whose seeds are too large for the remaining frugivores to disperse (Brodie 2017; Donoso et al. 2020; Galetti et al. 2013; Lim et al. 2020; Onstein et al. 2018). Ultimately, changes in trait matching may lead to reduced ecosystem functioning, including seed dispersal (Campagnoli et al. 2025; Cordeiro and Howe 2003; Donoso et al. 2020) and carbon storage (Bello et al. 2015; Chanthorn et al. 2019). Hence, the disruption of size-matching mechanisms by human disturbances is likely to reduce both the quality and quantity of seed dispersal outcomes.

Nevertheless, while defaunation causes downsizing, biotic invasions—including large-sized animals such as cattle, game and feral species—may also dominate in environments with high human disturbance. These animals may upsize frugivory networks, potentially leading to increased trait matching (but see Campagnoli et al. 2025; Heinen et al. 2023). Such invasions have been shown to homogenise plant–frugivore networks globally in terms of species identity (Fricke and Svenning 2020), and may either increase or decrease trait diversity, depending on the native species (Nowak et al. 2025). However, as our results show that human disturbance weakens rather than strengthens trait matching, invasive species are unlikely to shape our findings. Still, they may explain additional variation in trait matching, similar to the effects of latitude (e.g., seasonality) (Zhang et al. 2025) and island–mainland contrasts (Huang et al. 2025).

4.2 | Wet and Productive Environments Support Stronger Trait Matching by Increasing the Degree of Frugivory Within Plant–Frugivore Networks

The hypothesis that environmental conditions indirectly influence trait matching was supported by our SEMs. Precipitation and NPP were found to directly affect the average degree of frugivory per network, suggesting that animals that depend heavily on fruits (with a higher proportion of fruit in their diet) more strongly increase trait matching than animals that include items other than fruit in their diet. These results provide insights into how trait matching may arise from environmental dynamics that promote the evolution of endozoochorous fruits, increase the abundance of plants with edible fruits and subsequently increase the degree of frugivory in local animal assemblages (Kissling et al. 2009; Vasconcelos et al. 2023; Waide et al. 1999). Indeed, wet and productive environments—such as tropical rainforests—can sustain assemblages with a high diversity of fleshy fruits and frugivores (Fleming et al. 1987; Jordano 2000; Sinnott-Armstrong et al. 2018). This diversity may have resulted from resource partitioning or co-evolutionary dynamics through selection and specialisation on size-related traits (Albrecht et al. 2018; Onstein et al. 2017).

Interestingly, we did not detect any clear biogeographical structure in trait matching (Figure 3c), suggesting that deep time processes of trait evolution (e.g., Wölke et al. 2023) are less critical for trait matching patterns than contemporary processes, primarily human disturbance (as evidenced by the strongest effect size in the SEM, Figure 4). Alternatively, co-evolved trait matching patterns have been similar across regions due to the convergence of traits in plants and animals. For example, small and large fruits as well as small and large body sizes have evolved repeatedly and independently on all continents, and variation is primarily shaped by human impact, which lacks spatial structure. Spatial structure may therefore be more apparent at higher spatial resolution and smaller extents. Finally, a lack of structure may also be caused by factors such as interactions with invasive species, missing interaction data and sampling heterogeneity (Fricke and Svenning 2020).

5 | Limitations

In our synthesis, we made several assumptions that could influence the trait matching patterns we detected. First, because the dataset lacked consistent records of interaction frequencies, we relied on bipartite binary network data. However, trait matching itself may increase the frequency of certain interactions (Burns 2013; Dehling et al. 2014). By assigning equal weight to each pairwise interaction, we likely underestimated, rather than overestimated, the strength of trait matching. This approach may obscure finer ecological dynamics, as plant and frugivore species with strong mutualistic dependence, often reflected in frequent interactions, are treated similarly to those with infrequent interactions.

Second, sampling effort and method varied across networks, which could have biased trait matching estimates. For example, interactions with large vertebrates are particularly challenging to record, especially when these species are rare (Vidal et al. 2013). Additionally, extreme trait mismatches may have excluded certain species from the sample, such as large-fruited plants that, although present in the environment, may no longer rely on frugivores for seed dispersal due to the decline of large-bodied dispersers. Seeds from these 'ghost fruits' now often germinate beneath parent trees or rot away (Godfrey et al. 2008). As a result, such plant species can be underrepresented in plant–frugivore networks and may face extinction debt due to limited dispersal and the clumped spatial distribution caused by a breakdown in dispersal processes (Albert-Daviaud et al. 2020; Godfrey et al. 2008; Guimarães et al. 2008). Although we did not detect systematic changes in trait matching strength linked to sampling method (e.g., transect walks, animal tracking, mist netting, Figure S7) and addressed sampling effort by a weighting scheme to improve the reliability of Pearson's r estimates, other sampling aspects and context (e.g., temporal variation, season, duration, taxonomic focus, Quintero et al. 2022) may explain additional variation in trait matching across networks, especially at local scales. Furthermore, we acknowledge that using network size alone to correct species richness for sampling effort risks conflating biological signals (e.g., regions with high species richness) with sampling artefacts.

Third, trait matching is most relevant in the context of endozoochory; however, not all seed dispersal interactions conform to strict size matching, nor do they require endozoochory. For instance, some plant–disperser interactions involve epizoochory or stomatochory, such as parrots inadvertently dispersing tiny seeds on their beaks after feeding on sticky fruit pulp, a process that operates independently of size-based constraints (Hernández-Brito et al. 2021). Moreover, many frugivory interactions may not result in effective seed dispersal, as seeds are often destroyed rather than dispersed through such antagonistic interactions (e.g., seed predation) (Marques Dracxler and Kissling 2022; Simmons et al. 2018). To mitigate this limitation, we performed a sensitivity analysis by restricting the dataset to interactions involving animal species whose degree of frugivory (% fruit consumption) was equal to or greater than their degree of granivory (% seed consumption). This increased the likelihood that the retained interactions represented a proportionally greater amount of seed dispersal. Results from this filtered dataset were quantitatively and qualitatively similar to those obtained from the full analysis (Figure S5). Nevertheless, this approach cannot fully account for differences in fruit-handling behaviour among frugivores. For instance, mashers and pulp peckers may not engage in endozoochory despite high fruit intake (Marques Dracxler and Kissling 2022; Simmons et al. 2018). Consequently, species with similar degrees of frugivory can contribute differently to seed dispersal outcomes. Future studies should integrate measures of seed dispersal effectiveness (sensu Schupp et al. 2010), including qualitative aspects of interaction outcomes, to more accurately link functional traits with dispersal processes. Part of the unexplained variance in trait matching observed in our analysis likely reflects differences in the prevalence of specific fruit-handling behaviours across ecological networks. Despite these limitations, our synthesis reveals a clear global pattern of trait matching across tropical plant–frugivore networks.

6 | Conclusions

Our results demonstrate that plant–frugivore trait matching is a widespread macroecological pattern and that the disruptive impact of human activities on trait matching via downsizing is nearly twice as strong as the (indirect) effect of the environment. As large animals continue to decline in abundance and diversity (Dirzo et al. 2014; Ripple et al. 2019)—reminiscent of the extinction waves seen during the Late Quaternary—many large-fruited plants are at risk of losing their primary seed dispersal interaction partners, with detrimental consequences for the ecosystem functioning of tropical forests (Bello et al. 2015; Chanthorn et al. 2019; Donoso et al. 2020). Our work contributes to the growing body of trait-based research in plant–animal mutualisms (Bender et al. 2018; Dehling et al. 2014; Durand-Bessart et al. 2023; McFadden et al. 2022; Schleuning et al. 2020) and could be expanded by including additional traits, such as fruit colour, scent or chemistry (e.g., Pizo et al. 2021; Sinnott-Armstrong et al. 2018), to further elucidate the drivers and consequences of weakening trait matching in mutualistic networks. Additionally, we suggest that future research should investigate the remarkable intraspecific variation in fruit size consumption observed among frugivores across various networks (Figure 3a). This variation could provide valuable insights into the flexibility and adaptability of fruit-eating animals in response to environmental or human-induced changes in food availability, shedding light on how frugivorous species may adjust their foraging behaviour and diet as a result of changing ecological conditions.

Author Contributions

R.E.O., A.C. and D.G. designed the study, benefiting from discussions with W.D.K., E.F. and F.L. D.G. and M.P. contributed to data collection. D.G. performed data analyses and prepared figures. D.G. and R.E.O. drafted the initial manuscript, and all authors contributed to the final version. R.E.O. and A.C. supervised the study.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and analytical workflow (R script) necessary to replicate the analyses are available in the Supporting Information (Datasets S1–S4) and in Dryad: https://doi.org/10.5061/dryad.g1jwstr3h. This includes plant–frugivore interaction data (Dataset S1), plant trait data (Dataset S2), frugivore trait data (Dataset S3) and network data, including network-level trait matching, human disturbance and environmental conditions (Dataset S4).

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.70274.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ele70274-sup-0001-FigureS1-S7-TableS1.pdf. **Dataset: S1.** Network_Plant_Frugivore_Complete. **Dataset: S2.** Fruit_and_Seed_Traits. **Dataset: S3.** Frugivore_Traits. **Dataset: S4.** Network_TraitMatch_Env_v2.