Seed dispersal is a key process affecting the structure, composition and spatial dynamics of plant populations. Numerous plant species in the tropics rely upon animals to disperse their seeds. Humans have altered mammalian movements, which will likely affect seed dispersal distances (SDD). Altered SDD may have a range of consequences for plant communities including reduced seedling recruitment and plant biomass, seed trait homogenization, altered gene flow and a reduced capacity to respond to environmental changes. Therefore, modelling the consequences of altered animal behaviour on ecosystem processes is important for predicting how ecosystems will respond to human impacts. While previous research has focused on the link between animal species extirpation and SDD, it remains unclear how changes in mammalian movement will impact SDD. Here we implemented a mechanistic modelling approach to examine how mammalian movement reductions impact SDD in the tropics. We combined allometric theory with a mechanistic seed dispersal model to estimate SDD via the movement of 37 large frugivorous mammals (> 10 kg) in the tropics under different levels of human footprint, a global proxy of direct and indirect human disturbances. Our results suggest that assemblage-level SDD reductions are estimated to be up to 80% across the tropics in response to human disturbance. This is particularly the case in areas with high human impact such as agricultural landscapes and suburban areas. The region with the largest reductions in SDD was the Asia-Pacific with average reductions of 25%, followed by Central–South America (16%) and then Africa (15%). Our study provides insights into how human-induced changes in movement behaviour of large mammals could translate into altered ecosystem functioning.

Keywords: animal-mediated seed dispersal, ecosystem functions, frugivore, human impacts, individual-based model, mammal

Introduction

Seed dispersal is the movement of seeds away from the source plant and plays a fundamental role in the structure, composition and spatial arrangement of plant communities. Seed dispersal also facilitates key processes in plant ecology...
including reproduction, migration, colonisation and invasion (Levin et al. 2003). The dispersal of seeds across a landscape can confer additional benefits to plants including a reduction in competition, parasitism and predation (Janzen 1970, Howe and Miriti 2004). Dispersal is also important for providing plants with the capacity to respond and adapt to a changing environment – mitigating local declines in plant fitness via transport to more suitable habitat elsewhere (Corlett and Westcott 2013, Mokany et al. 2014). Human-induced processes such as habitat loss and hunting, can alter animal behaviour and in turn seed dispersal. Altered animal behaviour could therefore have a profound influence on ecosystem composition in a changing world.

Zoochory or animal-mediated seed dispersal is an important process for the dispersal of seeds, where endozoochory or the dispersal of seeds via ingestion (e.g. fruit seeds), is one of the key seed dispersal processes in tropical forests (Howe and Smallwood 1982, Gautier-Hion et al. 1985, Iluz 2010). Zoochory can shape the spatial configuration and composition of plant communities, in addition to facilitating the expansion of current populations and the foundation of new populations (Sasal and Morales 2013). For example, animal-mediated dispersal is important for plant communities in mosaic landscapes where animals maintain seed movement across the landscape (Matias et al. 2010). Zoochory may also confer fitness benefits by improving seed dispersal success by aiding the breakdown of the outer seed coating during digestion, and providing a nutrient-rich microhabitat for seeds to grow (e.g. defecation) (Hämäläinen et al. 2017). Animal-mediated seed dispersal is particularly important for long-distance dispersal (LDD) events, which are infrequent, but have a strong influence on large-scale processes such as gene flow and speciation (Ronce 2007, Travis et al. 2013). LDD is also important for plant communities in terms of connecting disparate populations, range expansion and coping with climate change (Trakhtenbrot et al. 2005, Nathan et al. 2008a).

Zoochory arises from patterns in foraging and movement of animals (Sasal and Morales 2013, Viana et al. 2016, Donoso et al. 2017, Fricke et al. 2018). Therefore, any changes to animal behaviour, distribution, traits and population density will likely translate into changes in seed dispersal patterns and ultimately impact plant communities. Human-induced alteration of composition of animal communities, such as changes in the number of individuals or species has been shown to impact seed dispersal patterns (Fontúrbel et al. 2015). In particular, LDD has been significantly reduced by defaunation or species loss (Donoso et al. 2020). Previous work has demonstrated that the loss of megafauna (i.e. species > 44 kg) has reduced seed dispersal distance in the tropics, particularly impacting LDD events, where the percentage of seeds from type I megafauna plants (i.e. fleshy fruits 4–10 cm in diameter with up to five large seeds) dispersed over one kilometre declined from > 40% to ~5% (Guimarães et al. 2008, Pires et al. 2018). Carpenter et al. (2018) found that the introduction of non-native animal species in New Zealand (e.g. rodents and feral pigs) caused a decline in a key ground-dwelling seed disperser (weka; Gallirallus australis), leading to declines in seed dispersal (~48% reduction) and increased seed predation (~10% increase). Several studies have further shown that a reduction in the number of frugivorous animals has negative impacts on plant species (i.e. reduced seed dispersal and seedlings) relying on animal-mediated seed dispersal (Wright et al. 2000, Brodie et al. 2009).

While previous work has predominantly focused on the impacts of the extirpation or decline of animal species on seed dispersal, it is possible that behavioural changes could also impact seed dispersal patterns (Fontúrbel et al. 2015, Nield et al. 2019, Morán-López et al. 2020). The ability of animals to move links the spatial dimension of individual behaviour to the ecological community (Lundberg and Moberg 2003, Nathan et al. 2008b). With an increasing human population and the related anthropogenic modification of habitats globally, there have been declines in animal movement, with reductions of 30% on average (Tucker et al. 2018). This decline is attributed to a combination of anthropogenic factors, including barriers that restrict movement, an increase in local food resources that reduce the need of individuals to move, and the loss of mammalian species that carry out long-distance movements (Tucker et al. 2018). Due to the link between animal movement and ecological functions, it is likely that changes in animal movement will impact seed dispersal (Nathan et al. 2008a). However, it is unclear how human impacts on animal movement will affect seed dispersal patterns.

About 70–90% of tropical plant species depend upon animal-mediated seed dispersal (both primary and secondary) (Howe and Smallwood 1982, Gautier-Hion et al. 1985), but we lack empirical understanding of how human-mediated changes in animal movement could influence seed dispersal distances (further referred to as SDD) in the tropics. Collecting data on animal-mediated seed dispersal in the field can be difficult and it is not currently possible to compare multiple animal species across their entire geographic range using field data. As an alternative, we can model seed dispersal by combining the available data on seed ingestion, gut passage time and animal movement with allometric theory to parametrise an individual-based model (IBM). IBMs can simulate individuals with different attributes and behaviours (e.g. body mass and movement patterns), where population- or community-level patterns emerge from these individuals interacting with each other and their environment (i.e. bottom–up models; DeAngelis and Grimm, 2014). IBMs are therefore a useful tool for exploring animal-mediate seed dispersal across the tropics.

Our aim was to examine how human impacts on animal movement will affect seed dispersal patterns in the tropics. Specifically, we assessed species-level SDD reductions at the population- and assemblage level, and examined the differences in the SDD reductions among different tropical regions. To achieve this, we modified an existing IBM (Pires et al. 2018) to simulate movements of 37 large mammalian frugivores (> 10 kg), who often comprise a large proportion of the vertebrate biomass in tropical regions (up to 85%; Estrada et al. 1993). The model included established
allometric equations for gut passage time and seed ingestion to model the spatial ecology of these 37 frugivores and seed dispersal in the tropics. The model also included an allometric movement equation for mammals, however, we modified this to account for the influence of the human footprint index and productivity (normalized difference vegetation index) on mammalian movement (i.e. step length), using the published data from Tucker et al. (2018). We also accounted for differences in ecosystem productivity in this movement equation because in areas with high productivity mammals (both cursorial and arboreal) tend to move less, as they can gather sufficient resources to meet their requirements over a smaller area, compared with mammals living in areas with low productivity (Isaac et al. 2014, Buchin et al. 2015, Tucker et al. 2018). We focused on the tropics as they experience high human disturbance (Benítez-López et al. 2017, Brinck et al. 2017, Gallego-Zamorano et al. 2020). We expected that the reduction in animal movement would result in a reduction in seed dispersal distance (SDD).

**Methods**

**Data**

We selected 37 mammal species that occur in the tropics to model SDD (Supporting information). We only included frugivorous mammals with a body mass of 10 kg or larger in our analysis, as the model is specifically developed for large seed-dispersing mammals (Pires et al. 2018). Frugivory was defined as species that eat > 50% fruit and seeds (Benítez-López et al. 2017) using the Elton traits database (Riede et al. 2011). We extracted mammal species’ range data from the IUCN (IUCN 2019), so that we could model SDD across the area in which the species are found. We excluded the elevations where the species are not found.

To model SDD, we required both trait and environmental data as they play an important role in not only shaping animal movement, but also the consumption of seeds. For each mammal species, we extracted body mass data (g) from the Elton traits diet database (Riede et al. 2011). We required environmental data including vegetation productivity and human impacts to model SDD (‘Mapping seed dispersal loss across the tropics’ section). As a proxy of vegetation productivity, we used the Copernicus 1 km PROBA-V global normalized difference vegetation index (NDVI) data (1999–2017 average; Jacobs and Wolfs 2019) and the 1 km global human footprint index (HFI for 2009; Venter et al. 2016). We used NDVI as our measure of vegetation productivity because it is commonly used in animal movement studies as a proxy of resources (including fruit) for different animal trophic levels (Willems et al. 2009, Mann et al. 2011, Pettorelli et al. 2011, Campos et al. 2014, Tucker et al. 2018). In addition, NDVI is often used in macroecological studies that span large geographic areas (i.e. temperate regions and the tropics) and multiple animal species as a measure of productivity, food resources and habitat selection (Chatterjee and Basu 2018, Ramirez-Bautista and Williams 2019). The typical range of NDVI values span −1 to 1, where values close to −1 represent water, and values less than 0.2 represent barren areas of rock, sand or snow (DeFries and Townshend 1994). Low, positive NDVI values represent shrub and grassland areas (~0.2 to 0.4). Values approaching 1, represent temperate and tropical rainforest areas. The mammal species included in our study come from a range of habitat types ranging from closed forests, to savanna resulting in a range of NDVI values from 0.2 to 0.9 (Supporting information).

We chose the HFI as our measure of human impacts because it is a global proxy of direct and indirect human disturbances, including roads, croplands, night-time lights and built environments. The HFI values can be assigned to five human pressure categories including ‘no pressure’ (HFI = 0), ‘low pressure’ (HFI = 1–2), ‘moderate pressure’ (HFI = 3–5), ‘high pressure’ (HFI = 6–11) and ‘very high pressure’ (HFI = 12–50) (Venter et al. 2016).

**Seed dispersal model**

We modified the equations and simulations from Pires et al. (2018) to examine the impact of human-related movement reductions on seed dispersal distance (SDD). Pires et al. (2018) developed an individual-based model (IBM) to estimate SDD by mammals. This IBM was run for individual mammal species to provide population-level SDD kernels, which were then further averaged across multiple species to provide assemblage-level SDD kernels. The IBM covers multiple species-specific components of the seed dispersal process, including seed ingestion (i.e. quantity of seeds consumed), seed retention (i.e. gut passage time) and animal movement (i.e. distance travelled over a period of time simulated using different movement models). These three seed dispersal processes are linked together by time from the start of the simulation to produce seed dispersal distance kernels (Fig. 1). For each species, we simulated the number of individuals using an established scaling relationship (Damuth 1981) to get a species-level population density value for each cell in their range (Pires et al. 2018). For each species, we also estimated the number of seeds ingested and the gut retention time based on the species-level retention times. For each individual, the number of seeds ingested was sampled from a Poisson distribution based on the average number of seeds ingested estimated using gut capacity (λ) and population density, both of which were determined using allometric relationships (Pires et al. 2018). Here, values represent the number of seeds ingested by individuals of a specific species in a single foraging event. Seed deposition times were based on gut retention times established from allometric relationships and were estimated for each individual seed consumed. Seed deposition times were sampled from a Gamma distribution, parameterised using the mean and variance of gut retention times based on previous work (Pires et al. 2018). Animal movement is then simulated using four different movement models that enabled us to
account for different movement strategies and to test the robustness of our results. We simulated movement as a random walk based on:

1. a Lévy walk (LW) as the default model, where movements have a high probability of short distances and a lower probability of longer step lengths (Bartumeus et al. 2005, Benhamou 2007);
2. a Brownian walk (BW), where movement is random in both distance and direction (Bartumeus et al. 2005);
3. a correlated random walk (CRW), where movement is correlated towards a specific direction such as a food source (Auger-Méthé et al. 2015); and
4. a composite correlated walk (CCRW), where movement has two distinct phases that includes area-restricted movements and nearly straight long-distance movements (Auger-Méthé et al. 2016).

The parameters used for the movement simulations can be found in the Supporting information. We focused on the Lévy walk model simulations in the main results, because these models are particularly valuable to understand distribution and dispersal over larger spatial scales (Pyke 2015).

In all four random walk simulations, we specifically modified the step length input to include human impacts. Using the published movement data from Tucker et al. (2018) for 41 terrestrial mammal species, we re-ran the linear mixed effects models exploring the relationship between movement distance, body mass, NDVI and HFI. We allowed random slopes and intercepts for NDVI and HFI at the order level (i.e. Artiodactyla, Carnivora, Diprotodontia, Lagomorpha, Perissodactyla, Primates and Proboscidea) to account for potential differences in the response of taxonomic groups based on differing ecologies. This resulted in seven order-specific equations with the structure (Supporting information):

$$\log_{10}(D) = \beta_0 + \beta_1 \times \log_{10}(BM) + \beta_2 \times \text{NDVI} + \beta_3 \times \text{HFI}$$  (1)

where $D$ is the median displacement distance in 32 hours (km per 32 h), $\beta_1$ are the order-specific coefficient values, BM the weight of the animal (kg), NDVI is the mean normalized difference vegetation index (dimensionless) of the area that the animal is moving in, and HFI is the mean human footprint index value (dimensionless) of the area that the animal is moving in. Equation 1 provides the displacement distance at the 32-h time scale (i.e. the closest temporal resolution to 24 h), and we converted this to metres per hour for movement simulations (i.e. $D \times 1000/32$). The displacement distance values were subsequently used to determine the step length for the animal movement simulation section of the IBM. The movement distances from these simulations were then combined with the seed deposition time (based on gut retention time) to get population-level SDD distributions. This is possible because we know how far an animal has travelled at each time point a seed is deposited. These SDD distributions are based on the dispersal distances of all seeds deposited by all individuals in a population, and we get one population-level SDD distribution per species. We then extracted the median value of the SDD distributions as our final metric of SDD to measure general patterns of dispersal distances.

**Seed dispersal relationships**

As a large proportion of the variation in animal movement can be explained by body mass, NDVI and HFI, we used a statistical model to incorporate this information into an IBM that we subsequently applied to predict SDD across the tropics. To achieve this, we ran simulations for binned values of NDVI (0.2–1, 0.1 increments) and HFI (0–50, increments of 1) for each of the 37 species to estimate seed dispersal patterns under different NDVI and HFI conditions. We ran the simulations using binned values of HFI and NDVI (i.e. rounding to the nearest whole number) to reduce the simulation run time due to the large spatial scale of the study (i.e. millions of grid cells). To ensure that binning the continuous NDVI and HFI values did not impact our results, we compared the IBM results for three species using the continuous NDVI and HFI grid cell values, with those results using the binned values. The results using the continuous and binned values were similar (Supporting information). We excluded regions with bare ground (i.e. NDVI < 0.2; DeFries and Townshend 1994) from our analysis due to the limited tracking data in Tucker et al. (2018) from these areas. We repeated the simulations for each species 2500 times for each NDVI–HFI combination (i.e. 50 HFI values and 9 NDVI values). The movement of each individual was simulated until all of the ingested seeds were

---

**Figure 1. Schematic of the individual-based model simulating mammalian seed dispersal in the tropics. The simulation starts at time zero ($t_0$) and the time is recorded when a seed is deposited ($t_{\text{deposit}}$). Step length is determined by body mass, normalized difference vegetation index (NDVI) and the human footprint index (HFI). To get the seed dispersal distance kernels, the seed deposition times are combined with the animal movement times and distances to get dispersal distance.**

---

**Allometric Relationship**

Simulation

Seed ingestion

Gut retention time

Step length

Seed deposition

Animal movement

Seed dispersal distance

 kernel

Deposition Time ($t_{\text{deposit}}$)

Simulation Starts ($t_0$)

Time ($t_0$)

Seed ingestion

Gut retention time

Step length accounting for mass + NDVI + HFI

Seed deposition

Animal movement

Seed dispersal distance kernel

Figure 1. Schematic of the individual-based model simulating mammalian seed dispersal in the tropics. The simulation starts at time zero ($t_0$) and the time is recorded when a seed is deposited ($t_{\text{deposit}}$). Step length is determined by body mass, normalized difference vegetation index (NDVI) and the human footprint index (HFI). To get the seed dispersal distance kernels, the seed deposition times are combined with the animal movement times and distances to get dispersal distance.
Mapping seed dispersal loss across the tropics

To predict the potential seed dispersal patterns across the mammal species’ ranges, we used a mixed effect model using the results from the ‘Seed dispersal relationships’ simulations. This model included log_{10} SDD as the response variable and log_{10} body mass, NDVI, HFI, an interaction term between body mass and HFI as the predictor variables, and a random effect for taxonomy to account for the phylogenetic relationships between the species. We also allowed for random slopes and intercepts for NDVI and HFI for each order to account for potential differences in the response to NDVI and HFI based on differing ecology and life histories. We extracted the NDVI and HFI values across each species range using the collected global NDVI and HFI data (‘Data collection’ section; Supporting information). For each species, we calculated the median SDD across each grid cell in their range using the order-specific SDD mixed effects models, and the grid-specific NDVI and HFI values. For comparison, we also estimated grid-specific SDDs for each species without human impacts, where the HFI was set to zero. These results were then used to construct maps of seed dispersal with and without human impacts for each species. We then combined these species’ maps by calculating the average SDD for each grid cell based on the species present in that cell, to quantify human impacts on assemblage-level mammalian SDD across the tropics.

We estimated the effect of human impact on SDD by calculating the difference between the SDD maps (i.e. reduction in SDD (%)) that included human footprint versus models where human footprint was set to zero, i.e. (SDD_{ZeroFootprint} – SDD_{Footprint})/SDD_{ZeroFootprint} ∗ 100. All analyses were performed in R ver. 3.2.3 (x86_64-pc-linux-gnu 64-bit; <www.r-project.org>).

Results

Seed dispersal relationships

We developed order-specific models that predicted population-level SDD based on body mass, NDVI, HFI and an interaction term between body mass and HFI using the input from the IBM simulations (Supporting information). Overall, the results were similar across the four movement simulation types, with the order-specific slope values of the relationship between log_{10} SDD and HFI ranging from −0.151 to −0.155 across all movement simulations (Supporting information).

Mapping seed dispersal

The reduction in population-level SDD across the 37 mammal species ranged from 0 to 81% and the median values of the population-level reductions ranged from 6 to 32% (Fig. 2a–b). These population-level SDD values represent the potential SDD of seeds in each grid cell across the range of each species. To examine patterns across the tropics, we averaged the population-level SDD data to produce assemblage-level SDD values, which represent the average potential distance a seed could be dispersed assuming the seed could be removed by an individual of any of the 37 species in the area (i.e. grid cell). When accounting for potential community structure using the mammal species range maps, we found that assemblage-level seed dispersal reductions were predicted across the tropics, but the extent of this reduction was highly variable across the grid cells, spanning 0–80% (Fig. 3b). On average, assemblage-level SDD reductions were 16% for Central and South America, 25% for the Asia-Pacific and 15% for Africa.

Our results suggest there is spatial variation in the SDD reduction patterns across the tropics (Fig. 3), reflecting the spatial variation in the environmental (i.e. NDVI and human impacts) and trait data (i.e. body mass) across the regions (Supporting information). Mammals in Africa had the largest average body mass (1920 kg) and lowest average NDVI (0.56), followed by the Asia-Pacific (mass: 529 kg, NDVI: 0.69) and Central–South America (mass: 67 kg; NDVI: 0.64). Central America, the eastern section of South America and South-East Asia all demonstrated SDD reductions greater than 60%, reflecting areas with high HFI values and a range of NDVI values. The region with the highest reduction in the SDD occurred in the Asia-Pacific, which had the highest average HFI values (9) across the three regions. We also found SDD reductions for the Africa and Central–South America regions, both of which had similar average HFI values (5.4 and 5.8, respectively). When comparing the reduction in SDD maps across the four movement models, the CV values were < 2% (Supporting information), demonstrating that our results are robust.

Discussion

Interpretation

We explored how human-induced changes in animal movements may affect SDD performed by large (> 10 kg) mammalian frugivores in the tropics. Our results suggest that median reductions in assemblage-level SDD is 15%, with potential reductions of up to 80% due to human-induced shifts in mammalian movement patterns. Larger SDD reductions were common in areas with high human impact such as agricultural landscapes and suburban areas. Our results provide a first insight into how changes in animal behaviour – specifically movement patterns – could alter seed dispersal patterns in the tropics.

There are several possible consequences for plant communities related to these changes in seed dispersal patterns. SDD reduction and loss have been linked to changes in above-ground biomass of forests. Poulsen et al. (2013) found that
in forests where hunting occurs, mammal-dispersal distances were reduced by 22% and that the above-ground biomass was lower than in other forests where hunting did not occur (e.g. 301 versus 455 Mg ha). Poulsen et al. (2013) further predicted that human-modified animal–plant interactions would alter forest species composition, favouring plant species that are fast-growing with low wood density and subsequently reducing long-term carbon storage capabilities. Also, plant species with larger seeds tend to be more sensitive to changes in SDD and mammal compositions, due to larger mammal species disappearing first from communities (Vanthomme et al. 2010, Menke et al. 2012). This size-bias in sensitivity to changes in mammal compositions may result in an increase in the number of plant species with smaller seeds and may even lead to the homogenization of fruiting plant species across the tropics (Terborgh et al. 2008).

SDD plays a role in the spatial genetic structure and gene flow of plants. A reduction in SSD also means altered gene flow and reduced connectivity between plant populations, which has consequences for meta-population dynamics.
(Couvet 2002, Trakhtenbrot et al. 2005, Pérez-Méndez et al. 2018). On the Canary Islands, for example, a reduction in SDD by frugivores was related to changes in the fine-scale genetic structure of Neochamaelea pulverulenta, including an increase in intra-population spatial genetic structure (i.e. decreased genetic variation near the maternal tree; Pérez-Méndez et al. 2016). Genetic variation in plant populations is important for both the ability to cope with environmental changes and evolutionary potential, so any changes in the spatial distribution of this genetic variation could impact the persistence of plant populations (Kremer et al. 2012).

Our results suggest that increasing human-modifications to landscapes could reduce SDD, resulting in seed deposition closer to natal seed sources. In some cases, the deposition of seeds close to the natal source can lead to increased competition and reduced seedling recruitment, and reduced plant species diversity (Janzen 1970, Howe and Miriti 2004). However, in other cases (e.g. Barro Colorado Island, Panama), it has been shown that negative density-dependent recruitment of seedlings contributes to enhanced seedling diversity (Harms et al. 2000). This means that if a particular plant species occurs in high density, then the seeds of that species are less likely to become established seedlings, preventing the dominance of a single species and leading to a higher diversity of plant species (Wills et al. 1997).

Our results also provide additional evidence that the combination of reduced movement with changes such as declining body size and loss of diet/habitat specialists, may also be causing large shifts in functional trait composition of frugivorous mammal communities (Prescott et al. 2016, Tagg et al. 2020). These changes in trait composition can, in turn, impact frugivore–plant interactions by changing the size of seeds consumed, reducing the quantity and distance that seeds are dispersed, and altering the seed bank accumulation (Vidal et al. 2013, Oleksy et al. 2017). To get a better understanding of the relationship between seed dispersal and mammal species richness, future work should examine the link between habitat fragmentation, SDD and species diversity at different spatial scales (Fahrig et al. 2019, Watling et al. 2020).

Validity of the analyses

Our simulations provide a first indication of the magnitude of SDD change under different levels of HFI. We compared the SDD values produced by the simulations with those recorded in the wild (i.e. for populations where data was available) to ensure that our model was working correctly, where we expected that our SDD values would be shorter than the published values. For example, average field-measured SDD values for Asian elephants Elephas maximus is > 1.2 km (Campos-Arceiz et al. 2008), African elephants Loxodonta africana is > 1 km (Blake et al. 2009), bonobos Pan paniscus is 145–1886 m (Tsuij et al. 2010) and orangutans (Pongo abelii and Pongo pygmaeus) up to 1 km (McConkey 2018). In our study, median SDD values were 461–1899 m for Asian elephants, 312–1556 m for African elephants, 97–192 m for bonobos and 67–248 m for orangutans, suggesting that our model was working as designed.

While our model provided realistic results, the model can be further improved by including more relevant factors related to seed dispersal. For instance, our IBM does not account for mammal species interactions (e.g. between frugivores or predator–prey interactions), frugivorous species turnover, differences in the level of seed damage across frugivorous species, seed viability or germination rates of those dispersed seeds. We also did not account for species adaptation – either plant or animal – to human disturbance or the potential increase in invasive or non-indigenous species that may occur when niche space opens up, which could potentially mediate the changes in movement behaviour. We expect that species interactions and adaptations and the role of species turnover in human-modified landscapes would be an important next step to incorporate into the model. We also note that we focused on endozoochory (seed ingestion), however other forms of animal-mediated seed dispersal (e.g. epizoochory, synzoochory and dyszoochory) also play a role in the movement of seeds. Future work should focus on the development of more comprehensive IBMs that includes these additional components of animal-mediated seed dispersal.

Second, we did not specifically distinguish between natural and anthropogenic (e.g. crops) habitats, but we did account for differences in the level of human disturbance between natural and anthropogenic habitats via the inclusion of HFI. It is possible that some mammal species specifically avoid human-modified landscapes (e.g. agriculture) and this might also limit their movements, or reduce their movement probability (Fahrig 2007). We recommend that future research on SDD should aim to include improved environmental data that explicitly excludes unsuitable habitat and incorporates habitat structure, habitat specialisation (i.e. a measure of habitat plasticity) and more fine-scale resource availability (e.g. fruit availability).

Third, we only accounted for changes in animal movements in our SDD scenarios, however, reductions in SDD will differ when also accounting for changes in mammal abundance and composition due to the loss of species from a community. Our model accounted for species-level differences in mammal population density, but it has been shown that density can also vary within a species, where individuals of a species are not evenly distributed across their ranges and can vary in response to human impacts (Santini et al. 2018). This variation in abundance alters the relative contribution of each mammal species to seed dispersal and in turn alters the distribution of SDD. Currently, it is difficult to reliably predict how the abundance of species varies across their range, therefore we do not account for spatial variation in population abundance. The loss of species from a community is often uneven across traits or ecological strategies. For example, losses are often biased towards large-bodied species (Santini et al. 2017) leading to the decline or loss of long-distance seed dispersal as well as altering the quantity of seeds dispersed (McConkey et al. 2012, Donoso et al. 2020).
Ecological strategies often lost in response to human impacts include habitat specialists, slow-lived species and species with low fecundity (Cooke et al. 2019). The combination of mammal species loss and the alteration of mammal behaviour (i.e. movement patterns) will impact SDD and in turn will have consequences for plant communities. Therefore, it is important to develop tools that not only detect early signals of altered SDD patterns, but also account for multiple changes in frugivore populations (i.e. changes in traits and behaviour) and account for a combination of stressors impacting SDD (e.g. land use change and hunting).

Conclusions

We modified a general allometric framework linking animal movement to seed dispersal by incorporating behavioural responses of mammals to human impacts, thus providing an insight into how changes in movement could translate into altered ecosystem functioning. Our results suggest that changes in animal movement patterns in response to humans will likely have an impact on SDD and in turn plant communities in the tropics. With increasing human impacts across the tropics, it is likely that seed dispersal patterns will continue to change and this will have cascading consequences for the vegetation communities. Our results provide additional support for the importance of maintaining landscape connectivity under human landscape modification, not only for animal movement, but also plant communities (Damschen et al. 2019).

Data availability statement

The data and code used in this study are available at: <http://doi.org/10.5061/dryad.hmgqnk9g8> (Tucker et al. 2021).

Acknowledgements – Funding – MAT was supported by a Radboud Excellence Initiative Fellowship.

Author contributions

Marlee A. Tucker: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). Michela Busana: Formal analysis (supporting); Methodology (supporting); Writing – review and editing (equal). Mark A. J. Huijbregts: Conceptualization (equal); Methodology (supporting); Resources (lead); Writing – review and editing (equal). Adam T. Ford: Conceptualization (equal); Methodology (supporting); Writing – review and editing (equal).

References

Auger-Méthé, M. et al. 2015. Differentiating the Lévy walk from a composite correlated random walk. – Methods Ecol. Evol. 6: 1179–1189.

Auger-Méthé, M. et al. 2016. Evaluating random search strategies in three mammals from distinct feeding guilds. – J. Anim. Ecol. 85: 1411–1421.

Bartumeus, F. et al. 2005. Animal search strategies: a quantitative random-walk analysis. – Ecology 86: 3078–3087.

Benhamou, S. 2007. How many animals really do the Lévy walk? – Ecology 88: 1962–1969.

Benitez-López, A. et al. 2017. The impact of hunting on tropical mammal and bird populations. – Science 356: 180–183.

Blake, S. et al. 2009. Forest elephants: tree planters of the Congo. – Biotropica 41: 459–468.

Brinck, K. et al. 2017. High resolution analysis of tropical forest fragmentation and its impact on the global carbon cycle. – Nat. Comm. 8: 14855.

Brodie, J. F. et al. 2009. Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. – Ecol. Appl. 19: 854–863.

Buchin, K. et al. 2015. Deriving movement properties and the effect of the environment from the Brownian bridge movement model in monkeys and birds. – Mov. Ecol. 3: 18.

Campos, F. A. et al. 2014. Drivers of home range characteristics across spatiotemporal scales in a Neotropical primate, Cebus capucinus. – Anim. Behav. 91: 93–109.

Campos-Arceiz, A. et al. 2008. Behavior rather than diet mediates seasonal differences in seed dispersal by Asian elephants. – Ecol. Evol. 8: 5992–6004.

Chatterjee, S. and Basu, P. 2018. Food preferences determine habitat selection at multiple scales: implication for bird conservation in tropical forests. – Anim. Conserv. 21: 332–342.

Cooke, R. S. C. et al. 2019. Projected losses of global mammal and bird ecological strategies. – Nat. Comm. 10: 2279.

Corlett, R. T. and Westcott, D. A. 2013. Will plant movements keep up with climate change? – Trends Ecol. Evol. 28: 482–488.

Couvet, D. 2002. Deleterious effects of restricted gene flow in fragmented populations. – Conserv. Biol. 16: 369–376.

Damschen, E. I. et al. 2019. Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment. – Science 365: 1478–1480.

Damuth, J. 1981. Population density and body size in mammals. – Nature 290: 699–700.

DeAngelis, D. L. and Grimm, V. 2014. Individual-based models in ecology after four decades. – F1000Prime Rep. 6: 39.

DeFries, R. S. and Townshend, J. R. G. 1994. NDVI-derived land cover classifications at a global scale. – Int. J. Remote Sens. 15: 3567–3586.

Donoso, I. et al. 2017. Defaunation effects on plant recruitment depend on size matching and size tradeoffs in seed-dispersal networks. – Proc. R. Soc. B 284: 20162664.

Donoso, I. et al. 2020. Downsizing of animal communities triggers stronger functional than structural decay in seed-dispersal networks. – Nat. Comm. 11: 1582.

Estrada, A. et al. 1993. Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico. – In: Fleming, T. H. and Estrada, A. (eds), Frugivory and seed dispersal: ecological and evolutionary aspects. Springer, pp. 245–257.

Farhig, L. 2007. Non-optimal animal movement in human-altered landscapes. – Funct. Ecol. 21: 1003–1015.
Fahrig, L. et al. 2019. Is habitat fragmentation bad for biodiversity? – Biol. Conserv. 230: 179–186.

Fontürbel, F. E. et al. 2015. Meta-analysis of anthropogenic habitat disturbance effects on animal-mediated seed dispersal. – Global Change Biol. 21: 3951–3960.

Fricke, E. C. et al. 2018. Defaunation leads to interaction deficits, not interaction compensation, in an island seed dispersal network. – Global Change Biol. 24: e190–e200.

Gallego-Zamorano, J. et al. 2020. Combined effects of land use and hunting on distributions of tropical mammals. – Conserv. Biol. 34: 1271–1280

Gautier-Hion, A. et al. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. – Oecologia 65: 324–337.

Guimarães, P. R. et al. 2008. Seed dispersal anachronisms: rethinking the fruits extinct megafauna ate. – PLoS One 3: e1745.

Hämäläinen, A. et al. 2017. The ecological significance of secondary seed dispersal by carnivores. – Ecosphere 8: e01685.

Harms, K. E. et al. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. – Nature 404: 493–495.

Howe, H. F. and Miriti, M. N. 2004. When seed dispersal matters. – Bioscience 54: 651–660.

Howe, H. F. and Smallwood, J. 1982. Ecology of seed dispersal. – Annu. Rev. Ecol. Syst. 13: 201–228.

Iluz, D. 2010. Zoochory: the dispersal of plants by animals. – In: Dubinsky, Z. and Seckbach, J. (eds), All flesh is grass. Springer, pp. 199–214.

Isaac, B. et al. 2014. Simplification of arboreal marsupial assemblages in response to increasing urbanization. – PLoS One 9: e91049. IUCN 2019. The IUCN Red List of Threatened Species. Ver. 2019-2. – <www.iucnredlist.org> accessed February 2019.

Jacobs, T. and Wolfs, D. 2019. Normalized difference vegetation index: long term statistics 1 km: GLOBE 1999–2017 (V2.2.1). – <https://land.copernicus.eu/global/products/ndvi>, accessed 17 April 2019.

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. – Am. Nat. 104: 501–528.

Kremer, A. et al. 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. – Ecol. Lett. 15: 378–392.

Levin, S. A. et al. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. – Annu. Rev. Ecol. Evol. Syst. 34: 575–604.

Lundberg, J. and Moberg, F. 2003. Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. – Ecosystems 6: 87–98.

Mann, K. K. et al. 2011. Delineating productivity zones in a degraded mosaic landscape. – Restor. Ecol. 18: 619–627.

Matías, L. et al. 2010. Seed dispersal patterns by large frugivorous mammals in a degraded mosaic landscape. – Restor. Ecol. 18: 466–492.

McConkey, K. R. et al. 2012. Seed dispersal in changing landscapes. – Biol. Conserv. 146: 1–13.

Menke, S. et al. 2012. Plant–frugivore networks are less specialized and more robust at forest–farmland edges than in the interior of a tropical forest. – Oikos 121: 1553–1566.

Mokany, K. et al. 2014. Loss of frugivore seed dispersal services under climate change. – Nat. Comm. 5: 3971.

Morán-López, T. et al. 2020. Can network metrics predict vulnerability and species roles in bird-dispersed plant communities? Not without behaviour. – Ecol. Lett. 23: 348–358.

Nathan, R. et al. 2008a. Mechanisms of long-distance seed dispersal. – Trends Ecol. Evol. 23: 638–647.

Nathan, R. et al. 2008b. A movement ecology paradigm for unifying organismal movement research. – Proc. Natl Acad. Sci. USA 105: 19052–19059.

Nield, A. P. et al. 2019. The spatial complexity of seed movement: animal-generated seed dispersal patterns in fragmented landscapes revealed by animal movement models. – J. Ecol. 108: 687–701.

Oleksy, R. et al. 2017. Flying foxes create extensive seed shadows and enhance germination success of pioneer plant species in deforested Madagascan landscapes. – PLoS One 12:e0184023.

Pérez-Méndez, N. et al. 2016. The signatures of Anthropocene defaunation: cascading effects of the seed dispersal collapse. – Sci. Rep. 6: 24820.

Pérez-Méndez, N. et al. 2018. Persisting in defaunated landscapes: reduced plant population connectivity after seed dispersal collapse. – J. Ecol. 106: 936–947.

Pettorelli, N. et al. 2011. The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. – Clim. Res. 46: 15–27.

Pires, M. M. et al. 2018. Pleistocene megafaunal extinctions and the functional loss of long-distance seed-dispersal services. – Ecography 41: 153–163.

Poulsen, J. R. et al. 2013. Ecological erosion of an Afro tropical forest and potential consequences for tree recruitment and forest biomass. – Biol. Conserv. 163: 122–130.

Prescott, G. W. et al. 2016. Reducing the impacts of Neotropical oil palm development on functional diversity. – Biol. Conserv. 197: 139–145.

Pyke, G. H. 2015. Understanding movements of organisms: it’s time to abandon the Lévy foraging hypothesis. – Methods Ecol. Evol. 6: 1–16.

Ramírez-Bautista, A. and Williams, J. N. 2019. The importance of productivity and seasonality for structuring small rodent diversity across a tropical elevation gradient. – Oecologia 190: 275–286.

Riede, J. O. et al. 2011. Stepping in Elton’s footprints: a general scaling model for body masses and trophic levels across ecosystems. – Ecol. Lett. 14: 169–178.

Rončec, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. – Annu. Rev. Ecol. Evol. Syst. 38: 231–253.

Santini, L. et al. 2017. Shifting baseline in macroecology? Unraveling the influence of human impact on mammalian body mass. – Divers. Distrib. 23: 640–649.

Santini, L. et al. 2018. Global drivers of population density in terrestrial vertebrates. – Global Ecol. Biogeogr. 27: 968–979.

Sasal, Y. and Morales, J. M. 2013. Linking frugivore behavior to plant population dynamics. – Oikos 122: 95–103.

Tagg, N. et al. 2020. Long-term trends in wildlife community structure and functional diversity in a village hunting zone in southeast Cameroon. – Biodivers. Conserv. 29: 571–590.

Terborgh, J. et al. 2008. Tree recruitment in an empty forest. – Ecology 89: 1757–1768.

Trakhtenbrot, A. et al. 2005. The importance of long-distance dispersal in biodiversity conservation. – Divers. Distrib. 11: 173–181.

Travis, J. M. J. et al. 2013. Dispersal and species’ responses to climate change. – Oikos 122: 1532–1540.
Tsuji, Y. et al. 2010. Estimation of seed dispersal distance by the bonobo, *Pan paniscus*, in a tropical forest in Democratic Republic of Congo. – J. Trop. Ecol. 26: 115–118.

Tucker, M. A. et al. 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. – Science 359: 466–469.

Tucker, M. A. et al. 2021. Data from: Human-induced reduction in mammalian movements impacts seed dispersal in the tropics. – Dryad Digital Repository, <http://doi.org/10.5061/dryad.hmgqmk9g8>.

Vanthomme, H. et al. 2010. Bushmeat hunting alters recruitment of large-seeded plant species in Central Africa. – Biotropica 42: 672–679.

Venter, O. et al. 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. – Nat. Comm. 7: 12558.

Viana, D. S. et al. 2016. Migratory birds as global dispersal vectors. – Trends Ecol. Evol. 31: 763–775

Vidal, M. M. et al. 2013. Large vertebrates as the missing components of seed-dispersal networks. – Biol. Conserv. 163: 42–48.

Watling, J. I. et al. 2020. Support for the habitat amount hypothesis from a global synthesis of species density studies. – Ecol. Lett. 23: 674–681

Willems, E. P. et al. 2009. Remotely sensed productivity, regional home range selection and local range use by an omnivorous primate. – Behav. Ecol. 20: 985–992.

Wills, C. et al. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. – Proc. Natl Acad. Sci. USA 94: 1252–1257.

Wright, S. J. et al. 2000. Poachers alter mammal abundance, seed dispersal and seed predation in a Neotropical forest. – Conserv. Biol. 14: 227–239.