



# Frugivory and Seed Dispersal by Carnivorans

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Seed dispersal is critical to the ecological performance of sexually reproducing plant species and the communities that they form. The Mammalian order *Carnivora* provide valuable and effective seed dispersal services but tend to be overlooked in much of the seed dispersal literature. Here we review the literature on the role of Carnivorans in seed dispersal, with a literature search in the Scopus reference database. Overall, we found that *Carnivorans* are prolific seed dispersers. *Carnivorans'* diverse and plastic diets allow them to consume large volumes of over a hundred families of fruit and disperse large quantities of seeds across landscapes. Gut passage by these taxa generally has a neutral effect on seed viability. While the overall effect of *Carnivorans* on seed dispersal quality is complex, *Carnivorans* likely increase long-distance dispersal services that may aid the ability of some plant species to persist in the face of climate change.

**Keywords:** carnivore, seed dispersal, carnivoran, frugivory, endozoochory

## INTRODUCTION

Seed dispersal is a crucial process that allows populations of sexually reproducing plants to persist locally, improve fitness and gene flow, and shift or expand their geographic ranges (Howe and Smallwood, 1982; Levin et al., 2003). Understanding the dispersal mechanisms in sexually reproducing plants is, therefore, crucial for understanding current plant distributions and community composition, as well as predicting future distributions and compositions (Harper, 1977; Howe and Smallwood, 1982). Natural selection has favored the evolution of fleshy fruits or fleshy accessory structures (hereon referred to as fruits), in turn these fruits encourage the consumption of a plant's seeds by animals who then disperse the seeds providing a fitness benefit (Tiffney, 1984; Tiffney, 2004; Eriksson, 2016), a process called endozoochory. The pattern of dispersal *via* endozoochory is influenced by how seed traits interact with disperser traits. Furthermore, the behaviors, life-history traits, and physiology of *Carnivora* make them distinct from other dispersers. For example, *Carnivora* often maintain large home ranges (i.e., ursids, Graham and Stenhouse, 2014), gut passage times are long (Escribano-Avila et al., 2014; Draper et al., 2021) which will affect the patterns of seedfall across landscapes and the consequences of those patterns in ways that differ from other frugivores (Schupp and Fuentes, 1995; Jordano et al., 2007; Martínez et al., 2008). Differences in seed disperser gut-passage time and post-consumption movement can influence

dispersal distances, while their habitat use and defecation patterns can influence micro-site characteristics and degree of seed clumping that will influence plant recruitment. Therefore, it is important to understand the full complement of seed dispersers on the landscape. In this review, we discuss the unique role of an often-overlooked group of endozoochoric seed dispersers, species in the order *Carnivora*.

To date, most research on seed dispersal *via* endozoochory has focused on taxa outside the order *Carnivora*, primarily birds and other mammals such as primates and bats. For example, a Scopus search on January 5, 2022 of seed disp\* AND (bird OR mammal OR carniv\*) returned 3,486 studies, of which only 164 focused on taxa in the order *Carnivora*. This focus on other taxa is in part because of the colloquial view that most *Carnivorans* are largely meat-eaters, leading to the assumption that they likely play only an indirect and incidental role in seed dispersal through their effects on their frugivorous prey (e.g., Hämäläinen et al., 2017). However, the order *Carnivora* is a hyperdiverse group of animals that includes 13 families of land dwellers whose diet's range from nearly obligate meat-eaters (e.g., species in the family *Felidae*) to omnivores (e.g., black bears, *Ursus americanus*) to strict herbivores (e.g., pandas, *Ailuropoda melanoleuca*, Atwood et al., 2020). Although seed dispersal studies have concentrated on other taxa, there is growing evidence that several species of *Carnivorans* are effective and important seed dispersers (Willson, 1993; Enders and Vander Wall, 2012; Spennemann, 2019). Furthermore, the behaviors, life-history traits, and ecologies of *Carnivora* make them distinct from other dispersers such as birds and other mammals (e.g., Escribano-Avila et al., 2014; Selwyn et al., 2020). Thus, to obtain a more complete understanding of plant distributions and population and community dynamics across space and time, we must understand *Carnivorans* role as seed dispersers.

In this paper, we review the role *Carnivorans* play in seed dispersal. First, we examine the prevalence of observed and potential endozoochoric seed dispersal by species in the order *Carnivora*. Second, we examine the importance of *Carnivoran* seed dispersal under two frameworks: seed dispersal effectiveness (SDE) and long-distance dispersal (LDD). The SDE framework measures effective seed dispersal as an interaction of quality (viable seeds, suitable deposition locations etc.) and quantity (the number of seeds dispersed), while LDD is defined as dispersal beyond the seed source stand or beyond the genetic neighborhood that produced the seed (Schupp, 1993; Schupp et al., 2010; Jordano, 2017).

We conducted a review of the literature using the Scopus reference database (November 2020). Our search used 396 pairs of search terms that paired frugivory/seed dispersal terms with a *Carnivoran* terms including Latin names and common names (**Supplementary Table 1**). This returned a total of 1,746 papers; 1,406 papers were removed due to an irrelevant double meaning of a search term or a lack of peer review. An additional 62 papers were removed that looked exclusively at seed predation such as the consumption of acorns and other hard mast, or diplochory of seeds in the stomach of prey. Ultimately, 278 papers met our complete search criteria (**Supplementary Table 2**). In reviewing

this literature, we found that *Carnivorans* are effective and prolific seed dispersers across the globe.

## PREVALENCE OF FRUGIVORY IN CARNIVORA

We found that frugivory and seed dispersal are common among taxa in the order *Carnivora*, occurring in at least 10 families (**Table 1** and **Supplementary Table 2**). Research noting frugivory and seed dispersal by members of the family *Canidae* (e.g., coyotes, foxes, and wolves) were the most common (33% of studies), while another 28% of studies focused on members of the family *Mustelidae* (e.g., martens, *Martes*). Studies on frugivory in *Viverridae* (e.g., civets, *Civettictis*), *Ursidae* (e.g., bears, *Ursus*), and *Procyonidae* (e.g., raccoons, *Procyon*) were also prevalent in the literature, while *Mephitidae* (e.g., skunks, *Mephitis*), *Herpestidae* (e.g., mongoose, *Herpestes*), *Hyaenidae* (e.g., hyenas, *Hyaena*), *Ailuridae* (red panda, *Ailurus*), and *Nandiniidae* (African palm civet, *Nandinia*) were represented by four or fewer studies each. The limited number of frugivory studies on these particular groups of *Carnivora* does not necessarily mean that they play only a minor role in seed dispersal, but instead could reflect research or publication biases. However, based on their ecology, some *Carnivorans* are unlikely to consume fruits intentionally. For example, no studies identified frugivory or seed dispersal in members of *Felidae* (cats), *Prionodontidae* (lisang), or *Eupleridae* (fossa), which are known to consume little to no plant parts (Atwood et al., 2020). These three taxa also lack a functional sweet taste, reducing the likelihood that they would be attracted to consuming fruits (Jiang et al., 2012). Diet studies on *Carnivorans* also often group all plant parts together or include plant parts in the diet category “other,” likely underestimating the extent of *Carnivoran* frugivory. Thus, consumption of fruits and dispersal of seeds by *Carnivorans* is surely higher than documented in the literature.

Many species of *Carnivora* are opportunistic foragers that switch diets depending on prey availability and vulnerability (Chavez-Ramirez and Slack, 1993; Santos et al., 2003; Takahashi et al., 2008; Zhou et al., 2008). This diet plasticity allows many *Carnivora* to increase their consumption of fruits when they are readily available or during times when other prey are scarce (Silva et al., 2005; Takahashi et al., 2008). Notably, the diets of some species of *Carnivora*, such as coyotes and bears, can be dominated by fruits at certain times of the year (Dumond et al., 2001; Takahashi et al., 2008). Additionally, *Carnivoran* frugivory is influenced by the diverse physical capabilities of taxa within the order. Species capable of climbing commonly consume fruits directly from trees (*Viverridae*, *Ursidae*, *Mustelidae*, Mudappa et al., 2010; García-Rangel, 2012; Takatsuki et al., 2018), while other species are dependent on fruits falling to the ground (*Canidae*, *Mustelidae*, Herrera, 1989; Grünwald et al., 2010) or consuming fruits from low bushes that are accessible from the ground (*Ursidae*, Belant et al., 2010; Harrer and Levi, 2018). This diversity of foraging strategies within and across *Carnivoran* families is demonstrated in the diversity of plant species and fruit types they consume. We found documentation of *Carnivorans*

**TABLE 1** | Breakdown of the distribution of studies we found in our literature search described in the introduction by family and genus, and whether those studies looked at seed dispersal or frugivory in each taxonomic group.

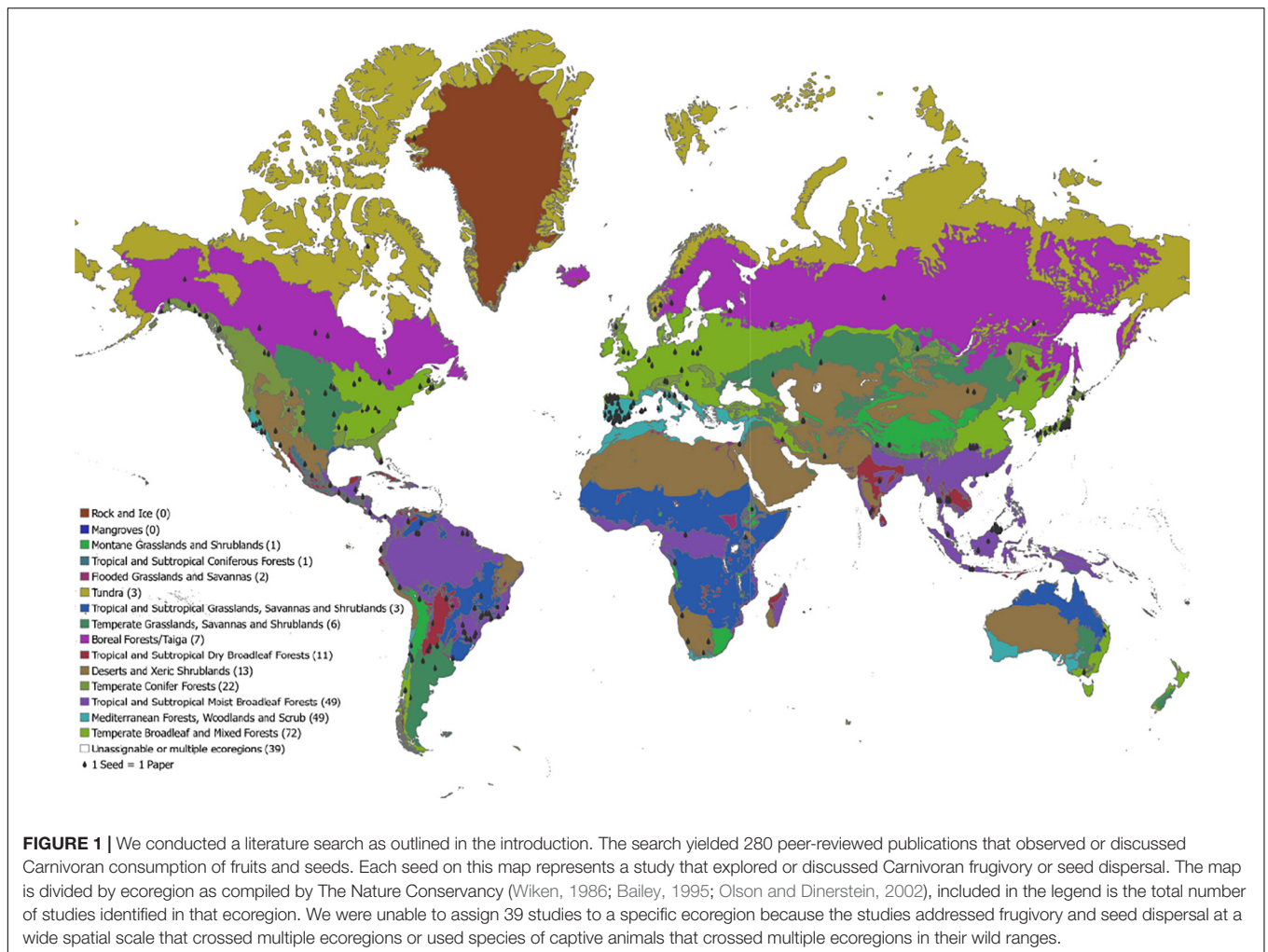
Family	Genus	Total	Frugivory	Seed dispersal
Canidae		150	55	95
	<i>Atelocynus</i>	1		1
	<i>Canis</i>	26	10	16
	<i>Cerdocyon</i>	9	4	5
	<i>Chrysocyon</i>	3	2	1
	<i>Cuon</i>	1	1	
	<i>Lycalopex</i>	19	7	12
	<i>Nyctereutes</i>	14	9	5
	<i>Otocyon</i>	3		3
	<i>Urocyon</i>	10	4	6
	<i>Vulpes</i>	64	18	46
Mustelidae		126	48	78
	<i>Eira</i>	4	2	2
	<i>Lutra</i>	1	1	
	<i>Martes</i>	71	26	45
	<i>Meles</i>	36	14	22
	<i>Melogale</i>	3		3
	<i>Mustela</i>	9	5	4
	<i>Neogale</i>	1		1
	<i>Neovison</i>	1		1
Viverridae		59	29	30
	Not specified	1		1
	<i>Arctictis</i>	10	7	3
	<i>Arctogalidia</i>	2	2	
	<i>Civettictis</i>	3	1	2
	<i>Cynogale</i>	1	1	
	<i>Genetta</i>	6	2	4
	<i>Hemigalus</i>	1	1	
	<i>Paguma</i>	12	6	6
	<i>Paradoxurus</i>	13	5	8
	<i>Prionodon</i>	1	1	
	<i>Viverra</i>	4	2	2
	<i>Viverricula</i>	5	1	4
Ursidae		60	25	35
	Not specified	1		1
	<i>Helarctos</i>	4	2	2
	<i>Melursus</i>	1		1
	<i>Tremarctos</i>	2	2	
<i>Ursus</i>	52	21	31	
Procyonidae		46	28	18
	<i>Bassaricyon</i>	1	1	
	<i>Bassariscus</i>	5	3	2
	<i>Cerdocyon</i>	1		1
	<i>Nasua</i>	14	8	6
	<i>Potos</i>	6	6	
<i>Procyon</i>	19	10	9	
Mephitidae		4	3	1
	<i>Conepatus</i>	2	1	1
	<i>Mephitis</i>	1	1	
<i>Spilogale</i>	1	1		
Herpestidae		2	0	2
	<i>Herpestes</i>	2		2
Hyaenidae		2	2	2
	<i>Hyaena</i>	2	2	
Ailuridae		1	1	0
	<i>Ailurus</i>	1	1	
Nandiniidae		1	1	0
	<i>Nandinia</i>	1	1	

Publications that studied multiple genera or families are counted in this table as separate studies for each genus.

consuming the pomes, drupes, berries, arils, or dry cones of at least 118 families of plants, with *Rosaceae* (e.g., blackberries), *Moraceae* (e.g., mulberry), and *Ericaceae* (e.g., heather) being the most prevalent in the literature (Supplementary Table 3). However, we did not identify any plant species that were solely dependent on seed dispersal by a *Carnivoran*. We also found that *Carnivora* exploit species of fruits with which they share a long history of co-occurrence, as well as novel fruits (Cypher and Cypher, 1999; Mudappa et al., 2010; Roehm and Moran, 2013). The consumption and dispersal of seeds from familiar and novel fruits suggest that *Carnivora* could increase the spread of fruit-bearing invasive plant species (Spennemann, 2019), as well as alter the dispersal patterns of native fruit-bearing plants encountered by novel *Carnivoran* species that are experiencing range expansion (e.g., coyotes, Hody and Kays, 2018). This is particularly important given that defaunation will limit plants' abilities to track a suitable niche in the changing climate (Fricke et al., 2022); therefore the natural introduction of a novel generalist seed disperser may re-establish climate tracking for some plants.

The geographic locations of studies exploring frugivory in the order *Carnivora* suggest that they are prolific seed dispersers across the globe (Figure 1). Frugivory or seed dispersal by at least one *Carnivoran* species has been documented on every continent, except Antarctica. Most studies on *Carnivoran* frugivory or seed dispersal have taken place in North America, South America, Europe, and East Asia (e.g., Japan and parts of Malaysia), with fewer studies on *Carnivoran* frugivory or seed dispersal in Africa, Oceania, and western Asia. The lack of studies in Oceania likely stem from there being few native *Carnivorans* in this region, although two studies from Australia suggest that the introduction of *Carnivorans* to new regions could result in new mutualistic relationships with native (or invasive) plants (Brunner et al., 1976; O'Connor et al., 2020). The few studies in Africa and Central/Western Asia are somewhat surprising considering that IUCN's Red List shows 119 and 53 species of *Carnivora*, respectively across these regions (IUCN, 2021). As a result, the geographic prevalence of *Carnivora* seed dispersal could be much greater than the literature currently suggests, especially in Africa and parts of Asia.

In addition to being globally widespread, *Carnivoran* frugivory or seed dispersal has been documented in every terrestrial ecoregion (Wiken, 1986; Bailey, 1995; Olson and Dinerstein, 2002), except mangroves and rock/ice (Figure 1). Most studies have been conducted in temperate, tropical, and subtropical regions. In particular, there is a greater number of studies focusing on *Carnivoran* frugivory or seed dispersal in temperate/broadleaf mixed forests, Mediterranean forests/woodlands/scrubs (mostly in Spain), and tropical and subtropical moist broadleaf ecoregions. In general, the number of studies investigating *Carnivoran* frugivory was lowest in polar regions. Fewer studies in higher latitude systems could reflect a reduction in the prevalence of omnivory with increasing latitudes, or a reduction in the number of *Carnivoran*-fruiting plant combinations that could be studied due to reduced species diversity at the poles (Hillebrand, 2004). Regardless, the global expanse of documented *Carnivoran* frugivory combined with the



taxonomic breadth of the plant species consumed suggests that if the seeds consumed by members of *Carnivorans* are viable, then *Carnivora* are likely prevalent and important seed dispersers throughout the globe.

## CONSEQUENCES OF CARNIVORAN SEED DISPERSAL

Two distinct yet overlapping concepts can help guide our thinking about the consequences of seed dispersal by *Carnivorans*: SDE and LDD events. These frameworks can be integrated with demographic models (Beckman et al., 2020) to predict how seed dispersal by *Carnivorans* influences the persistence and spread of plant populations.

### Seed Dispersal Effectiveness

Seed dispersal effectiveness has been defined as the contribution a seed disperser makes to the fitness of a plant it disperses. While this is ideally measured in terms of the recruitment of new reproductive adults to the population, empirical studies generally quantify disperser contributions to the performance

of some earlier life-history stage, such as successful seedling establishment, rather than new adults (Schupp, 1993; Schupp et al., 2010; Schupp et al., 2017). SDE has a quantity component and a quality component, where  $SDE = \text{quantity} \times \text{quality}$ . Quantity is the number of seeds dispersed and quality is the probability that a dispersed seed successfully produces a new adult. In terms of the quality of seed dispersal by *Carnivorans*, we highlight: (1) the treatment in the mouth and gut, (2) the local distance dispersed, and (3) the seedscape, that is, the local environmental factors that influence recruitment after seed deposition (Beckman and Rogers, 2013).

### Quantity of Seed Dispersal

When thinking about the consequences of seed dispersal by *Carnivorans*, the quantity of seed dispersal is straightforward – it is simply the number of seeds dispersed and *Carnivorans* generally consume large quantities of fruit per feeding (Harrer and Levi, 2018; Shakeri et al., 2018). However, quantity is also influenced by the total number of visits by a disperser, and we know much less about this. *Carnivoran* visitation can be facilitated when other herbivores and frugivores improve the accessibility of fruits by removing thorny vegetative parts or

knocking fruits off of trees, thus increasing dispersal quantity (Selwyn et al., 2020). Quality, however, is more complex and can be affected by a variety of outcomes of the *Carnivoran*-plant interaction as discussed next.

### Quality of Seed Dispersal: Treatment in the Mouth and Gut

When frugivores feed on fruits there is a continuum of outcomes, from all seeds being treated gently and dispersed physically intact to all being destroyed by chewing or by gut passage itself (Schupp, 1993). For seeds that do pass through the gut intact, seed germinability may be reduced or increased and germination timing may be altered (Traveset, 1998). Gut passage may increase seed germination by scarifying seed coats either chemically or mechanically, potentially reducing physiological or physical seed dormancy (Traveset et al., 2007; Soltani et al., 2018). Furthermore, fecal matter can protect seeds from predators or pathogens and provide fertilizer (Traveset et al., 2007). Consequently, what happens during gut passage can have negative, positive, or neutral consequences for the quality component of SDE.

Consumption of fruits by *Carnivorans* typically results in intact seeds being passed through the digestive system and deposited in scat (Herrera, 1989; Perea et al., 2013). Destruction of seeds by chewing generally occurs when the seeds are ground in the mouth. However, even highly frugivorous *Carnivoran* species like bears (Harrer and Levi, 2018) have a dentition that is optimized for a diverse omnivorous diet (Elbroch, 2006). As a result, the molars in *Carnivorans* are specialized for crushing (i.e., bones and hard mast) rather than grinding (Elbroch, 2006), making the breaking of seeds, especially smaller seeds, less likely in *Carnivorans* (Koike et al., 2008; Lalleroni et al., 2017). Furthermore, fruits are often consumed whole and processed in the stomach of *Carnivorans*, allowing for the passing of even large seeds intact (e.g., *Prunus*; Rogers and Applegate, 1983). Every study within our literature search that quantified the proportion of seeds that were passed found that greater than 90% of seeds were passed intact (**Supplementary Table 4**). These studies included members of the families *Canidae*, *Mustelidae*, *Ursidae*, and *Viverridae*, with no clear variation in seed treatment by different *Carnivoran* families. Studies that included dry fruited or nut species accounted for the highest proportion of broken seeds, while most seeds from fleshy fruited species were defecated with greater than 98% of seeds intact (**Supplementary Table 4**).

Although most *Carnivorans* appear to pass seeds intact, the effect of gut passage on seed viability, germination, and dormancy is less straightforward. *Carnivoran* gut passage of intact seeds generally shows a neutral effect on viability; 70.6% of studies (defined as each seed-*Carnivoran* pair as some papers explored multiple interactions) showed that viability was maintained at the same proportion as undigested seeds, and more than 167 additional studies showed that seeds were viable after dispersal however without a control comparison to evaluate proportional changes in seed viability (**Supplementary Table 4**). In some cases, gut-passage can help break seed dormancy or alter germination timing, with examples showing both accelerated and delayed germination as illustrated in the distribution of studies

in our review (49% accelerating, 13.7% delaying, and 37.3% resulting in no change in germination timing **Supplementary Table 4**). However, the effect of gut passage on seed viability and germination can be species-pair-specific (Traveset and Willson, 1997; Rubalcava-Castillo et al., 2021), with the same seed species being affected differently by different *Carnivoran* species, and vice-a-versa. Altering germination timing and proportions has the potential to create a mismatch between germination and favorable conditions for recruitment while depleting viable seeds from the seed bank and decreasing future recruitment (Traveset et al., 2007; Roehm and Moran, 2013). Alternatively, these alterations in germination timing can also lead to beneficial alignment between germination and recruitment conditions resulting in higher overall recruitment (Traveset et al., 2007). Therefore, changes in germination timing are not necessarily positive or negative, but context-dependent depending on plant species, ecoregion, and past and future climate and weather. Studies to date that look at viability and germination are heavily biased toward *Canidae* and *Ursidae*. The variability in seed responses and low representation of *Carnivoran* taxa studied necessitates further research on *Carnivoran* seed dispersal to elucidate broad and consistent trends.

### Quality of Seed Dispersal: Local Dispersal

The local distance seeds are dispersed from the parent can have a large effect on the quality of dispersal and overall SDE. Dispersal away from the parent plant frequently increases survival and successful recruitment through escape from distance- and density-dependent seed and seedling enemies that concentrate attack beneath and near adult conspecifics (e.g., Janzen, 1970; Connell, 1971; Howe et al., 1985; Schupp, 1988; Comita et al., 2014). Often, the advantage is not simply getting away from the parent, but rather the advantage steadily increases with increasing distance from the parent or other conspecific adults (Howe et al., 1985) provided seeds are deposited in a suitable microsite for germination and establishment. How far a frugivore disperses seeds is dependent on gut-passage time and the distance and directionality of travel by the disperser.

Despite the importance of gut-passage time for understanding the capabilities of an effective seed disperser, few studies have investigated gut-passage time in *Carnivorans* (**Table 2**). In our limited dataset, average gut-passage times for *Carnivorans* that have consumed fruit ranged between 2.5 and 18 h (**Table 2**), with maximum gut-passage times exceeding 24 h for several *Carnivoran* species. Of the species studied, Japanese marten (*Martes melampus*) had the shortest average gut-passage times of 2.5 h, and Asiatic black bear (*Ursus thibetanus*) had the longest average gut-passage time of 18 h (Koike et al., 2011; **Table 2**). Gut-passage times roughly scale with body size ( $p$ -value = 0.01,  $r$ -squared = 0.54, **Figure 2**). However, one factor that might affect gut-passage times in individual *Carnivorans* is diet composition; diets containing more fruit likely have shorter gut-passage times. For example, one study found that an increase in fruit in brown bear (*Ursus arctos*) diets reduced the average gut-passage time from 14.5 to 6.5 h (Elfström et al., 2013). Conversely, there was no effect of the proportion of fruit in the diet on gut-passage times for coyotes (Draper et al., 2021). Though gut-passage time

**TABLE 2** | Animal body mass, average gut-passage time, and the range of gut-passage time of Carnivoran species identified as frugivores/seed dispersers.

Species	Mass (kg)	Gut-passage time (h)	Gut-passage time range (h)	Source
<i>Procyonidae Potos flavus</i>	3.00	2.50	0.7–5.6	Smith et al., 2003; Lambert et al., 2014
<i>Mustelidae Martes melampus</i>	1.00	5.50	0.6–51.7	Smith et al., 2003; Tsuji et al., 2015
<i>Mustelidae Martes americana</i>	1.25	4.30	3.8–10.3	Hickey et al., 1999; Smith et al., 2003
<i>Ursidae Ursus arctos</i>	180.52	5.78	4.6–7.0*	Smith et al., 2003; Elfström et al., 2013
<i>Viverridae Arctictis binturong</i>	9.88	6.50	3.3–9.3	Smith et al., 2003; Grassman et al., 2005
<i>Canidae Lycalopex gymnocercus</i>	4.54	6.80	5.5–8.1	Varela and Bucher, 2006; Jones et al., 2009
<i>Canidae Cerdocyon thous</i>	5.24	7.70	4.5–13.0	Smith et al., 2003; Varela and Bucher, 2006
<i>Canidae Nyctereutes procyonoides</i>	4.04	8.83	4–32.8	Smith et al., 2003; Mise et al., 2016
<i>Canidae Canis latrans</i>	13.41	14.82	2.0–36.0	Smith et al., 2003; Draper et al., 2021
<i>Ursidae Ursus thibetanus</i>	77.50	18.90	3.2–44.3	Smith et al., 2003; Koike et al., 2011

All values are for adults of both sexes. All reported gut-passage times are for mixed or pure fruit diets. Species with multiple records are reported as a mean of the data included therein.

\*1st and 3rd quantiles reported in paper rather than first and last defecation.

may be altered when consuming fruit for some species (both decreasing and increasing gut-passage time, Cipollini and Levey, 1997), passage times remain on the order of hours suggesting that regardless of how much fruit was consumed, *Carnivorans* physiology can accommodate long dispersal distances.

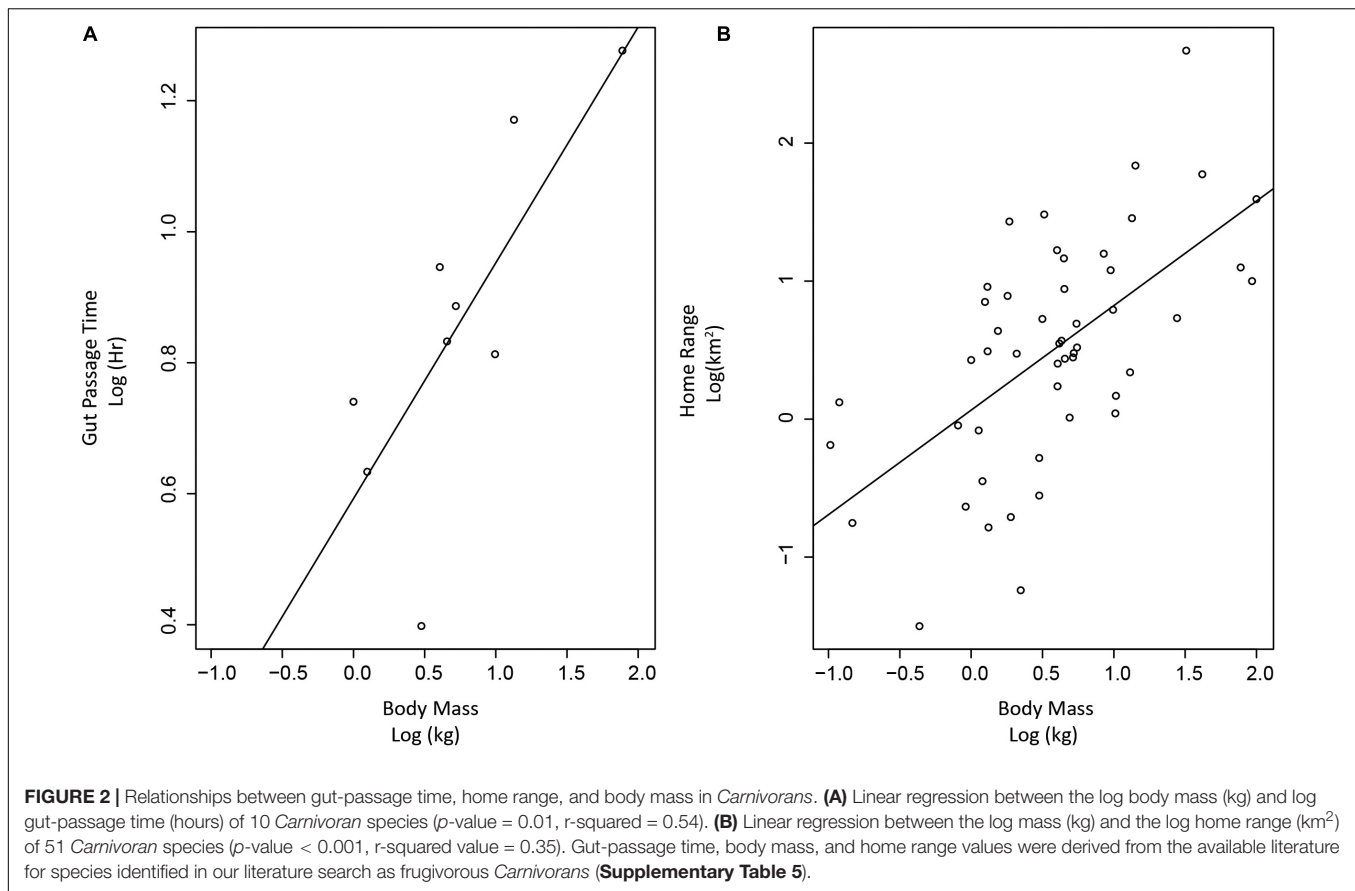
Seed dispersal distances provided by *Carnivorans* have been shown to correlate with the maximum movement possible within the animal's home range (González-Varo et al., 2013). Movements by *Carnivorans* are often constrained to an individual's home range because many species are territorial (Gese and Ruff, 1997; Graham and Stenhouse, 2014). *Carnivorans* travel extensively within their home range to maximize access to resources, avoid risks from intraspecific and intraguild aggression (Hertel et al., 2019), and engage in territorial marking and patrolling (Gese and Ruff, 1997; Graham and Stenhouse, 2014). While there can be a wide variation in home range size within a species, daily total movement tends to stay the same across a population, with animals with smaller home ranges utilizing the entire space daily, and those with larger home ranges traversing it over multiple days with similar daily travel distances (Goszczyński, 2002). Similar to gut-passage time, home range size also increases with *Carnivoran* body size ( $p$ -value < 0.001,  $r$ -squared value = 0.35; **Figure 2** and **Supplementary Table 5**). Therefore, we expect *Carnivoran* seed dispersal to also scale with body size. Considering that the body size of documented fruit-eating *Carnivorans* spans three orders of magnitude, from the least weasel (*Mustela nivalis*; 0.10 kg) to the brown bear (*Ursus arctos*; 180.5 kg), we would expect that *Carnivorans* express a multitude of different dispersal distances. Thus, *Carnivorans* are likely diverse in their abilities to disperse seeds away from the parent plant and other conspecifics that may compete with seedlings.

### Quality of Seed Dispersal: The Seedscape

Beyond removal from the vicinity of maternal plants, an additional aspect of local dispersal services is the ecological conditions into which seeds are deposited. *Carnivorans* deposit seeds in different habitats than many other seed dispersers, providing seed dispersal that is complimentary to other dispersers that results in a more diverse seedscape (Beckman and Rogers, 2013). *Carnivoran* behavior such as patrolling and territorial

marking can lead to the deposition of seed-laden scat along travel corridors (Suárez-Esteban et al., 2013; Rubalcava-Castillo et al., 2020) and in open habitats either as a marking or coincidentally as they pass through (Gese and Ruff, 1997; Rost et al., 2012; Fedriani et al., 2018). In contrast, other endozoochoric dispersers (e.g., passerines) and abiotic dispersal generally result in seed deposition within contiguous canopy cover with high fruit occurrence (Jordano and Schupp, 2000; Herrera and García, 2010; Escribano-Avila et al., 2014). The deposition of seeds in travel corridors and open habitats provides seed dispersal to sites that are often either in completely novel habitat or along habitat edges, complementing other dispersal vectors. Furthermore, *Carnivorans* increase dispersal into open habitats improving colonization and recolonization of disturbed habitats better than their avian counterparts (Escribano-Avila et al., 2014). The complimentary dispersal patterns provided by *Carnivorans* can improve the fitness of the plants that they disperse (Celedón-Neghme et al., 2013; Escribano-Ávila et al., 2013; Escribano-Avila et al., 2014). However, this diversity of deposition also has the potential to negatively affect the outcome for seeds that are ultimately dispersed to unsuitable habitats.

*Carnivorans* broadcast seeds widely at a macro scale (i.e., meters to kilometers, González-Varo et al., 2013) by traveling long distances before defecating seeds, but concentrate them at a micro scale (sub 1 m, Shakeri et al., 2018) by concentrating them in a single scat. These patterns can alter their effects on SDE quality (Schupp et al., 2002). The majority of studies in our literature search observing *Carnivoran* seed consumption and deposition record a large number of seeds per scat (e.g., Matias et al., 2010; Harrer and Levi, 2018; Shakeri et al., 2018). The concentration of many seeds into a single deposition can reduce the quality component of SDE. Seeds suspended within an intact scat have lower rates of emergence (Draper et al., 2021), so the extent to which secondary dispersers remove seeds and distribute them elsewhere will affect the ultimate quality of dispersal (Enders and Vander Wall, 2012). Concentrating seeds in a single location can also attract seed predators (which are often also secondary dispersers) and increase the spread of pathogens, countering some of the many benefits that dispersal provides (LoGiudice and Ostfeld, 2002; Shakeri et al., 2018). Furthermore,



the release of many seeds in a single scat can increase the potential for future competition among seedlings and juvenile plants (Loiselle, 1990; Schupp et al., 2002). Some *Carnivoran* species in the families *Canidae*, *Procyonidae*, *Nandiniidae*, *Mustelidae*, and *Viverridae* can further compound the above effects on quality by depositing scats in spatially discrete latrines, potentially resulting in extremely large concentrations of seeds (Clevenger, 1996; Page et al., 1999; Page et al., 2001; Helbig-bonitz et al., 2013; Osugi et al., 2020). Conversely, a clumped rather than even distribution of seeds can result in higher rates of recruitment due to a lower ability of pathogens or predators to track vulnerable seeds (Beckman et al., 2012), and the fertilizing effect of scat can improve germination and recruitment conditions for seeds growing from scats and latrines, helping to overcome the negative effects of high seed and seedling density (O'Farrill et al., 2013; Sugiyama et al., 2018). The potential for both positive and negative effects of *Carnivoran* dispersal on SDE suggests that future studies should focus on monitoring the number of successful recruits to later life history stages, as opposed to the more common approaches that focus on seed viability and germination.

## Long-Distance Dispersal

Long-distance dispersal affects plant genetic exchange and migration (Jordano, 2017). LDD occurs when a seed is moved beyond the geographic limits of its source stand or outside

the genetic neighborhood of the source plant (Jordano, 2017). *Carnivorans* provide dispersal distances that move seeds beyond the threshold defining LDD for many plant species (Lalleroni et al., 2017; Spennemann, 2018; Pereira et al., 2019). With these LDD events *Carnivorans* aid in maintaining gene flow between disparate stands, improving genetic diversity and resiliency (Harper, 1977). Furthermore, by providing dispersal beyond the confines of a current plant stand, *Carnivorans* can aid in range shifts to track suitable climate conditions or recolonize disturbed landscapes (Escribano-Avila et al., 2014; Naoe et al., 2016). This will have the most profound effect in areas where *Carnivoran* species are repatriating former ranges (Draper et al., 2017) and re-establishing LDD services or where they are colonizing new territory and introducing a new LDD service (Hody and Kays, 2018).

## DISCUSSION

The geographic, taxonomic, and ecological breadth of *Carnivoran* frugivory and seed dispersal supports the hypothesis that *Carnivorans* are common and likely important seed dispersers worldwide. Given their sizes and gut capacities, many *Carnivorans* can consume large quantities of fruits and seeds in a feeding bout and thus have the potential to be quantitatively important seed dispersers. However, at this point we lack a full

understanding of the quantitative component of SDE provided by *Carnivorans* due to a paucity of data on the number of visits made to individual plants. Considering treatment in the mouth and gut, *Carnivorans* commonly pass fruit seeds intact and generally have a neutral effect on seed viability, while gut passage generally has neutral or positive effects on germination, indicating high quality treatment. When seeds are deposited, the scat itself provides fertilizer and protection from some seed predators and pathogens, clearly positive consequences of *Carnivoran* seed dispersal (Traveset et al., 2007; O’Farrill et al., 2013). In contrast, the concentration of seeds in *Carnivoran* scat and the latrine behavior of many *Carnivorans* has the potential to increase density-dependent seed predation (Shakeri et al., 2018) and increase conspecific and heterospecific competition among seedlings and juvenile plants. The long dispersal distances *Carnivorans* can provide potentially improves seed and seedling survival in the face of distance-dependent enemies. However, the biotic and abiotic characteristics of the sites where seeds are deposited often have a greater impact than distance on the quality of dispersal and this has been poorly addressed. Overall, although there is clear evidence that *Carnivoran* seed dispersal has the potential to be quantitatively and qualitatively effective, there are substantial gaps in our knowledge of both. Consequently, the overall SDE provided by Carnivorans is uncertain at this time.

The wide range of potential dispersal distances among different *Carnivorans* combined with other biotic and abiotic dispersal vectors adds to the portfolio of strategies that plants can employ to distribute their seeds across a landscape (Escribano-Avila et al., 2014). Relatively long gut-passage times combined with the potential to move long distances suggest that *Carnivorans* can provide regular LDD services. While this may sometimes carry seeds outside of quality germination conditions, it can also provide them the potential for range expansion and connect disparate populations of the same species to help maintain genetic diversity (Levine and Murrell, 2003). As a result, LDD by *Carnivorans* could play an important role in the ability of certain plant species to persist in the face of climate change (Kremer et al., 2012; Corlett and Westcott, 2013).

Perhaps the most intriguing and important aspect of *Carnivoran* seed dispersal is its potential complementarity with avian seed dispersal. Birds generally defecate or regurgitate

seeds while perched, depositing seeds beneath existing vegetation (Jordano and Schupp, 2000; Herrera and García, 2010). By contrast, many *Carnivorans* defecate and deposit seeds along travel routes and in open habitats, resulting in very different seed shadows than those produced by birds (Suárez-Esteban et al., 2013; Rubalcava-Castillo et al., 2020). Although deposition in open habitats is unlikely to be advantageous for all species, such a pattern of seed dispersal can promote more rapid range expansion and recolonization of disturbed habitats for those species able to recruit in these conditions (Escribano-Avila et al., 2014).

## AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

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