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Carnivoran Frugivory and its Effect on Seed Dispersal, Plant Community Composition, Migration, and Biotic Carbon Storage

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CARNIVORAN FRUGIVORY AND ITS EFFECT ON SEED DISPERSAL, PLANT COMMUNITY COMPOSITION, MIGRATION, AND BIOTIC CARBON STORAGE

by

John P. Draper

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Ecology

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ABSTRACT

Carnivoran Frugivory and its Effect on Seed Dispersal, Plant Community Composition, Migration, and Biotic Carbon Storage

by

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Utah State University 2022

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Department: Watershed Sciences

Dispersal patterns of plants influence their population genetics, connectivity, community dynamics, and ecosystem functioning. Animal mutualists that consume seeds can disperse them in unique patterns according to their ecologies; therefore, it is important to understand how differences between dispersers alter the pattern of seed rain. Some seed dispersers are underrepresented in the seed dispersal literature despite ample evidence they consume fruits and seeds, such as members of the order Carnivora. The overall goal of my dissertation was to describe the extent and quality of Carnivoran seed dispersal, quantify important variables surrounding seed dispersal for a specific Carnivoran, the coyote (Canis latrans), and estimate how differences in dispersal by coyotes and another sympatric seed disperser would affect plant community composition and biotic carbon storage. In chapter 2, I performed a systematic literature review of Carnivoran frugivory and seed dispersal. In chapter 3, I experimentally evaluated coyote gut passage time and effect on three different plant species seeds. Finally, in chapter 4, I modeled how differences in seed dispersal distances between coyotes and passerines (Passeriformes) would affect future distributions of a woody plant, the juniper (Juniperus), and how juniper expansion would affect biotic carbon storage. In chapter 2, I found that frugivory and seed dispersal is common in 10 of the 13 terrestrial Carnivoran genera, involves a diversity of plant species, occurs worldwide across most ecoregions, and rarely damages seeds or decreases seed viability and germination. Furthermore, in chapter 3 I found that coyotes retain seeds in their guts on average between 4 and 24 hours and deliver seeds that have the same viability and germination characteristics as undigested seeds. Given coyote travel speeds, these results suggest that coyotes regularly disperse seeds up to 5 km, which is substantially larger than sympatric passerine species. In chapter 4, I found that this difference will lead to 2.5 times greater range expansion of juniper in the next 80 years, and 3.4 times greater grassland conversion. Coyote-mediated grassland conversion will also result in a 1.1 Pg increase of biotic carbon storage. My findings show that understudied seed dispersers like Carnivorans can greatly impact plant ecology and ecosystem services, highlighting the need for further research on these taxa.

(174 pages)

PUBLIC ABSTRACT

Carnivoran Frugivory and its Effect on Seed Dispersal, Plant Community Composition, Migration, and Biotic Carbon Storage

John P. Draper

Seed dispersal by animals is important for the ecology of plants. It is particularly important to understand which animals are involved and how they move seeds differently from one another. Some seed dispersers are understudied despite ample evidence they consume fruits and seeds. This includes animals commonly referred to as carnivores in the order *Carnivora*. The overall goal of my dissertation was to describe the extent and quality of seed dispersal by *Carnivorans*, estimate important aspects of seed dispersal for a specific *Carnivoran*, the coyote, and estimate how differences between a coyote and songbirds affect where plants will occur in the future and if that changes how much carbon plants store on the landscape. To achieve these goals, I first systematically reviewed existing research on frugivory and seed dispersal by *Carnivorans*. Then, I experimentally evaluated how long it takes for seeds to pass through a coyote, and if the consumption of seeds by coyotes negatively affects seed germination or viability. Finally, I modeled how differences in the distances that coyotes carry seeds vs. songbirds affect plant migrations. I found that *Carnivoran* frugivory and seed dispersal are common, involve many plant species, and occur worldwide across most ecosystems. *Carnivorans* also rarely damage seeds or hamper seed viability and germination when they consume and disperse seeds. Furthermore, I found that coyotes generally take between 4 and 24 hours to pass seeds from the fruits they consumed and deliver seeds to new landscapes without harming them. Given coyote travel speeds, these results suggest that coyotes regularly disperse seeds up to 5 km. This seed dispersal distance is substantially greater than songbirds and led to a 2.5 times larger expansion of where junipers grew in models extending 80 years into the future. Coyote seed dispersal would also result in 3.4 times greater conversion of grasslands and an increase total biotic carbon storage by 1.1 Pg. My findings show that understudied seed dispersers like *Carnivorans* can greatly impact plant ecology and ecosystem services and highlights the need for further studies on the impacts of Carnivora on seed dispersal.

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CHAPTER 1

INTRODUCTION

Seed dispersal is a crucial life stage for plants that has landscape-level consequences. How plants are dispersed across a landscape influences plant survival, plant community composition, and ecosystem services (Levin et al. 2003). Many plant species have evolved to utilize animals as vectors of dispersal (Harper 1977). For animal-dispersed seeds, the physiology and movement ecology of the animal determines the pattern of dispersal across a landscape. Differences in dispersal patterns between sympatric seed dispersers can result in seeds being deposited in vastly different conditions and distances from the source, which will result in different outcomes for the seed and the dispersed plant population and local community (Levine and Murrell 2003, Schupp et al. 2010, Escribano-Avila et al. 2014). Changes in seed dispersal can result in either the loss or the introduction of woody plant species which can alter the gross amount of biotic carbon storage in an area (Fernandez et al. 2013, Bello et al. 2015). Recent studies on seed-dispersing animals have focused on how the loss of frugivores is likely to alter plant community composition resulting in a loss of carbon storage (Bello et al. 2015, Culot et al. 2017). In some cases, however, populations of seed dispersers are increasing and expanding their distributions (Scheick and McCown 2014, Hody and Kays 2018), which may offset losses or change how seeds are dispersed. Many seed dispersers that are increasing are also omnivorous species in the order *Carnivora*, a group that is relatively understudied regarding seed dispersal.

The movement of seeds away from a parent plant and conspecific can increase individual survival by helping seeds escape pests and predators that are attracted to concentrations of conspecifics and reducing intraspecific competition (Janzen 1970, Connell 1971, Comita et al. 2014). Plants have evolved multiple mechanisms to facilitate seed dispersal and maximize dispersal distance including utilizing wind, water, and animal dispersal vectors (Levin et al. 2003). Plants often provision fruit or fleshy accessory structures (hereafter fruit) to encourage the consumption and distribution of seeds by animals, which is known as endozoochory (Levin et al. 2003).

Despite their name implying a carnivorous diet, *Carnivorans* are important seed dispersers in North America (Willson 1993). Frugivory is common in many families in the order *Carnivora;* for example, frugivory has been observed in many species of *Canidae, Mustelidae,* and *Ursidae* across the globe (McConkey and Galetti 1999, Tsuji et al. 2011, Harrer and Levi 2018, Lanszki et al. 2019, Kamler et al. 2020). Many families of *Carnivorans* are non-obligate carnivores that demonstrate plasticity with their diets (i.e., omnivorous), shifting between food sources based on their availability or as a result of anthropogenic or natural disturbances that alter prey vulnerability to predation (Dumond et al. 2001, Santos et al. 2003, Silva et al. 2005). This opportunistic feeding behavior by many *Carnivorans* has resulted in seasonal consumption of fruits when they are readily available (Chavez-Ramirez and Slack 1993, Santos et al. 2003, Takahashi et al. 2008) or when animal prey abundance is low (Dumond et al. 2001, Santos et al. 2003, Silva et al. 2005).

Consumption of fruit by *Carnivorans* has the potential to be mutualistic if ingestion has a neutral or positive effect on seed viability and germination. For example, the consumption of persimmon (*Diospyros)* fruits by coyotes (*Canis latrans*), results in equal or increased rates of germination compared to un-ingested fruit (Everitt 1984, Cypher and Cypher 1999, Roehm and Moran 2013). Studies looking at *Carnivoran* dispersal of multiple plant species showed that the effects of *Carnivoran* consumption on seed germination varied across plant species, with most plant species experiencing higher germination rates (Rogers and Applegate 1983, Traveset and Willson 1997, Sreekumar and Balakrishnan 2002, Juan et al. 2006, Varela and Bucher 2006), but some species experiencing neutral (Zhou et al. 2008a, Maldonado et al. 2018) or lower germination rates (Auger et al. 2002, Graae et al. 2004). Differences in the effect of *Carnivoran* consumption on seed germination were related to differences in the consumer's gut chemistry and seed characteristics, such as seed coat thickness (Auger et al., 2002). Factors that can affect excessive exposure of seeds to stomach acid are variations in gut chemistry due to longer gut-passage times and different diet compositions (Auger et al. 2002). However, studies suggest that most seeds remain viable after passage by *Carnivoran* (Vergara-Tabares et al. 2018, Draper et al. 2021).

Carnivorans differ from other seed dispersers such as passerines (*Passeriformes*), who broadly co-occur with frugivorous *Carnivorans* and consume many of the same fruits. For example, *Carnivorans* deposit seeds at greater distances from the parent compared to passerines (Escribano-Avila et al. 2014). Increased dispersal distances allow for deposition in novel communities where a particular plant species may not yet be established. Differences in dispersal distances between *Carnivorans* and passerines have been linked to gut-passage time. On average gut-passage times for *Carnivorans* is between 2 and 19 hrs when feeding on fruit (Graae et al. 2004, Varela and Bucher 2006, Zhou et al. 2008a, Koike et al. 2011) while frugivorous birds such as passerines have a gut-passage time of between 10 and 30 min (Levey and Grajal 1991, Murray et al. 1994). Longer gut-passage time for *Carnivorans* combined with their large home ranges allows for potential dispersal distances of km away from the parent (Grünewald et al. 2010, Lalleroni et al. 2017). Even small *Carnivorans* like the red fox (*Vulpes vulpes*) average a dispersal distance of over 1 km and have been observed dispersing seeds to nearly 3 km (González-Varo et al. 2013). Conversely, average passerine dispersal favors distances of less than 50 m, with rare dispersals up to 700 m (Carlo et al. 2013).

Carnivoran seed deposition also differs from passerine dispersal in that *Carnivorans* deposit seeds into different habitats. *Carnivorans* can favor depositing seeds in open habitats such as grasslands or disturbed landscapes whereas passerines favor depositing seeds in forested landscapes that are often close to conspecific plants or the parent itself (Herrera and García 2010, Peredo et al. 2013, Escribano-Avila et al. 2014, López-Bao et al. 2015). *Carnivorans* have also been shown to deposit seeds sufficiently upslope from parent plants, which may aid the plant species in escaping local effects of climate change (Naoe et al. 2016, González-Varo et al. 2017). The translocation of seeds by *Carnivorans* into novel habitats does not necessarily ensure they will persist. For some plant species, *Carnivorans* disproportionately deposit seeds in habitats that are unsuitable for germination or seedling establishment (Zhou et al. 2008a, Enders and Vander Wall 2012, Cancio et al. 2016, 2017). Differences in seed dispersal patterns provided by *Carnivorans* are of particular interest as some species, such as black bears, are recolonizing habitat that they were previously extirpated from (Bales et al. 2005, Scheick and McCown 2014, Draper et al. 2017), while others, like coyotes, are expanding their ranges into entirely new areas (Hody and Kays 2018); this range expansion has the potential to influence seed dispersal by introducing and increasing the abundance of long-distance seed dispersal services to new landscapes.

When *Carnivorans* deposit seeds into viable novel habitats there is the potential for changes in plant community dynamics that could change plant diversity and the composition of the plant community. Seed dispersal patterns can affect many different aspects of plant community dynamics including geographic range, diversity, and composition (Levine and Murrell 2003, Snell et al. 2019). For example, the loss of frugivorous seed dispersers has been shown to reduce overall plant community richness through the loss of recruitment of plant species dependent on biotic dispersal (Terborgh et al. 2008, Harrison et al. 2013, Wandrag et al. 2017).

With the introduction of a new seed disperser, it is logical to assume that the opposite would occur, as deposition of seeds into new habitats can lead to colonization by previously absent plant species (Howe and Miriti 2006, Snell et al. 2019) and a cascade of effects on the plant community, habitat quality for animal species, and ecological functions and services (Coates et al. 2017, Filippelli et al. 2020).

One potential way in which *Carnivoran* seed dispersal may change plant communities is through the conversion of grasslands to savannas, shrublands, and woodlands acting as a vector for woody encroachment. *Carnivorans* consume seeds of woodier fruiting plants such as juniper (*Juniperus,* Chambers et al., 1999; Stricklan et al., 2020)*,* and tend to deposit these seeds into open areas that are dominated by grass species (Peredo et al. 2013, Escribano-Avila et al. 2014, López-Bao et al. 2015). If the newly deposited woody species can overcome both biotic (competition, predation) and abiotic (e.g., water, fire; Briggs et al. 2005, Van Auken 2009) filters in its new habitat it can become established and transition from seedling to a sapling. Woody encroachment can cause increases in aboveground woody biomass and decreases in plant species diversity (Ratajczak et al. 2012), which in turn can increase aboveground biotic carbon storage (Van Auken 2009, Eldridge et al. 2011, Ratajczak et al. 2012, Fernandez et al. 2013, Filippelli et al. 2020).

Animals can have many different effects on the carbon storage capacity of a landscape through herbivory, predation of herbivores, soil compaction, or seed dispersal (Schmitz et al. 2018). Existing studies of the effect of seed dispersers on carbon storage have focused on the removal of key seed dispersers. These studies have shown the removal of dispersers of fruiting species with larger fruits and seeds reduces aboveground carbon storage significantly in tropical rainforests (Bello et al. 2015, Peres et al. 2016, Culot et al. 2017). To date, no studies have looked at how increasing dispersal services by the arrival of a new dispersal vector and the resulting plant community conversion can affect aboveground carbon storage. In this dissertation, I will examine the role of *Carnivorans* as seed dispersers worldwide, as well as use a an expanding species in North America, the coyote, to model and explore the potential for omnivorous carnivores to act as seed dispersers and the differential effect that they can have as seed dispersers on woody encroachment and carbon storage under changing climate conditions.

In chapter 2, I review what is currently known about *Carnivoran* frugivory and seed dispersal. I undertook a systematic literature review of *Carnivoran* frugivory and seed dispersal to facilitate a broader understanding of both the ecology of *Carnivoran* seed dispersal and the current state of research on the topic. I explore the spatial extent of known *Carnivoran* frugivory around the world and across different ecoregions, highlighting regions where frugivory and seed dispersal is likely understudied. In this review, I also enumerate the breadth of frugivory within *Carnivorans*. Finally, utilizing the seed dispersal effectiveness framework (Schupp 1993, Schupp et al. 2010), I assess the general effectiveness of *Carnivorans* as seed dispersers. The findings in this chapter provide a comprehensive view of *Carnivoran* frugivory around the world and the effects that it has on seed dispersal.

In Chapter 3, I tested the efficacy of coyotes as seed dispersers by experimentally measuring gut passage time, post-consumption seed viability, and germination. To be able to more accurately understand the potential contribution of coyotes to seed dispersal, I measured how long seeds took to pass through the coyote gut, and if varying proportions of fruit altered gut passage time. I then measured if gut passage, diet composition, and duration of gut passage had any effect on seed viability and germination to determine if coyote frugivory reduced the quality of the seeds that they dispersed. Finally, to measure the potential importance of secondary dispersal by granivores of seeds from scats to scatter hoarded caches, I quantified the difference in germination timing and total germination between seeds impounded in whole scats and ones that were removed from scats. My findings further the scientific understanding of how coyotes can aid in seed dispersal for multiple plant species.

In chapter 4, I predict how different seed dispersers differentially affect the spread of juniper across the conterminous United States via forecast modeling, and how woody encroachment by juniper could alter biotic above-ground carbon storage. First, an ecological niche model was applied to the conterminous United States for seven species of juniper under both a moderate and an extreme climate change scenario. Using those maps as a canvas for potential dispersal, migration models were run using parameters modeling coyote and passerine seed dispersal. The total area of migration was calculated, as well as the total predicted encroachment into grasslands. The predicted area of encroachment was used to estimate the potential differences in the change in above-ground biotic carbon storage provided by each seed disperser. These findings are important for guiding plant species migration and carbon cycle modeling, given the continuing range expansion of coyotes and the loss of other seed dispersers.

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CHAPTER 2

FRUGIVORY AND SEED DISPERSAL BY *CARNIVORANS*[1]

Abstract

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 plant dispersal. 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.

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 predicting past, current, and future plant distributions and community composition (Harper 1977, Howe and Smallwood 1982). To disperse their seeds, many plant species have evolved fleshy fruits or fleshy accessory structures (hereon referred to as fruits) that encourage the consumption and dispersal of their seeds by animal mutualists (Dennis et al. 2007), a process called endozoochory. The pattern of dispersal via endozoochory is influenced by how seed traits interact with disperser traits. Thus, the

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behavior, life history, and ecologies of different animal dispersers will affect how and where seeds are distributed on a landscape (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 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*, such as birds and other mammals. For example, a Scopus search on 1/5/2022 of seed disp* AND (bird OR mammal OR carniv*) returned 3,486 number of 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 *Carnivoran's* role as seed dispersers.

In this paper, we review the role that *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 whether *Carnivorans* are effective seed dispersers by reviewing their documented effects on the quantity and quality of the seed dispersed, as well as the potential for long-distance dispersal. Ultimately, we find that *Carnivorans* are effective and prolific seed dispersers across the globe.

Prevalence of Frugivory in Carnivora

We conducted a systematic review (Grant and Booth 2009) that shows frugivory and seed dispersal is common among taxa in the order *Carnivora,* occurring in at least 10 families (Box 2.1, Table 2.1, Appendix A: Supplemental Table 1 and 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 *Carnivoran's* 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). Diet studies on *Carnivorans* also often group all plant parts together or include plant parts in the diet category “other”, either not estimating or likely underestimating the importance of frugivory. Thus, consumption of fruits and seed dispersal by *Carnivorans* may be 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. 2008b). 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). We found documentation of *Carnivorans* 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 (Appendix A: Supplemental Table 3). We also found that *Carnivora* exploited both 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).

The geographic locations of studies exploring frugivory in the order *Carnivora* suggest that they are prolific seed dispersers across the globe (Figure 2.1). 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 we did find two studies from Australia that 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). 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 2.1). 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 utilized suggests that if the seeds consumed by members of *Carnivorans* are viable, then *Carnivora* are likely prevalent and important seed dispersers throughout the globe.

Carnivoran Seed Dispersal Effectiveness

Two distinct yet overlapping concepts can help guide our thinking about the consequences of seed dispersal by *Carnivorans*: Seed Dispersal Effectiveness (SDE) and dispersal distance including local seedscapes and long-distance dispersal events (Beckman and Rogers 2013, Jordano 2017). 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.

SDE

SDE 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, 2017). SDE has a quantity component and a quality component, where SDE = quantity x quality. Quantity is the number of seeds dispersed and quality is the probability that a dispersed seed successfully produces a new adult.

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* may generally consume larger quantities of fruit per feeding than other frugivores, such as avian species. Quality, however, is more complex and can be affected by a variety of outcomes of the *Carnivoran*-plant interaction. Below we highlight three outcomes of dispersal that are particularly relevant when thinking about the quality of seed dispersal by *Carnivorans*: 1) the treatment in the mouth and gut, 2) the distance dispersed, and 3) the spatial patterns of seed deposition.

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 improve seed germination by scarifying seed coats either chemically or mechanically potentially reducing physiological or physical seed dormancy, and 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 of dispersal and 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 (Appendix A: Supplemental 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 (Appendix A: Supplemental Table 4).

Although, in general, most *Carnivorans* appear to pass fruit 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 *Carnivoran* seed pairings maintained viability, and more than 167 pairings dispersed viable seeds; Appendix A: Supplemental 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 Appendix A: Supplemental Table 4). However, the effect of gut passage on seed viability and germination can be species pair-specific (Traveset and Willson 1997, Antón et al. 2006, 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 future potential recruitment (Traveset et al. 2007, Roehm and Moran 2013). However, these alterations in germination timing can also lead to beneficial alignment between germination and recruitment conditions resulting in higher overall recruitment. Studies to date that look at viability and germination are heavily biased towards *Canidae* and *Ursidae*. The variability in seed responses and narrow representation of *Carnivoran* taxa studied necessitates further research on *Carnivoran* seed dispersal to find broad and consistent trends.

Distance dispersed

The distance seeds are dispersed from the parent can have a large effect on the quality of dispersal and overall SDE, discussed here, and on the potential for long-distance dispersal (LDD), discussed below. 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. How far a frugivore disperses seeds is dependent on gut-passage time and the distance and directionality traveled 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 2.2). We found that average gut-passage times for *Carnivorans* that have consumed fruit ranges between 2.5 and 18 hours (Table 2.2), with maximum gut-passage times exceeding 24 hrs for several *Carnivoran* species. Of the species studied, Japanese marten (*Martes melampus*) had the shortest average gut-passage times of 2.5 hrs and Asiatic black bear (*Ursus thibetanus*) had the longest average gut-passage time of 18 hrs (Koike et al. 2010, Table 2.2). Despite the paucity of studies on gut-passage time for fruit diets in *Carnivorans*, we found that gut-passage times roughly scales with body size (p-value =0.01, r-squared = 0.54, Figure 2.2). 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 times from 14.5 hrs to 6.5 hrs (Elfström et al. 2013). Conversely, Draper et al. (2021) found no effect of the proportion of fruit in the diet on gut-passage times for coyotes. Though gut-passage time 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 2.2, Appendix A: Supplemental 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 seedings.

The seedscape

In addition to providing long-distance dispersal services, *Carnivorans* deposit seeds in different habitats than other seed dispersers, providing a diverse seedscape (Beckman and Rogers 2013). *Carnivoran* behavior such as patrolling and territorial marking can lead to the depositing 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, complimenting 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). However, this diversity of deposition does have the potential to negatively affect the outcome for some of the seeds which are ultimately dispersed to unsuitable habitats.

Carnivorans broadcast seeds widely at a larger spatial scale (meters to kilometers, González-Varo et al., 2013), but concentrate them at a micro spatial scale (sub 1 m, Shakeri et al., 2018), which 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. Matías et al. 2010, Harrer and Levi 2018, Shakeri et al. 2018). The concentration of many seeds into a single deposition can reduce the qualitative aspect of SDE. Seeds suspended within an intact scat have lower rates of emergence (Draper et al. 2021), necessitating secondary dispersers to remove seeds and distribute them elsewhere

(Enders and Vander Wall 2012). Concentrating seeds in a single location can also attract seed predators 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 (Clevenger 1996, Page et al. 1999, 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 new adults added to the plant population, as opposed to the more common approaches that focus on seed viability and germination.

Long-Distance Dispersal

Long-distance seed dispersal 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 longer dispersal distances that move seeds beyond the threshold of 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).

Conclusion

The geographic and taxonomic breadth of *Carnivoran* frugivory and seed dispersal supports the hypothesis that *Carnivorans* are common and potentially important seed dispersers worldwide. Studies suggest that *Carnivorans* commonly pass fruit seeds intact and generally have a neutral effect on seed viability. The effects of *Carnivorans* on seed germination are more complex. The passage of seeds through a *Carnivoran* gut generally has neutral or positive effects on germination, with scat itself providing fertilizer and protection from some seed predators and pathogens (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 seed predation (Shakeri et al. 2018) and increase conspecific competition among seedlings and juvenile plants. Overall, the effects of *Carnivoran* dispersal on the quality aspect of SDE are somewhat ambiguous, and further studies should aim to resolve this question.

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 long-distance dispersal 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, long-distance dispersal 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).

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Figures

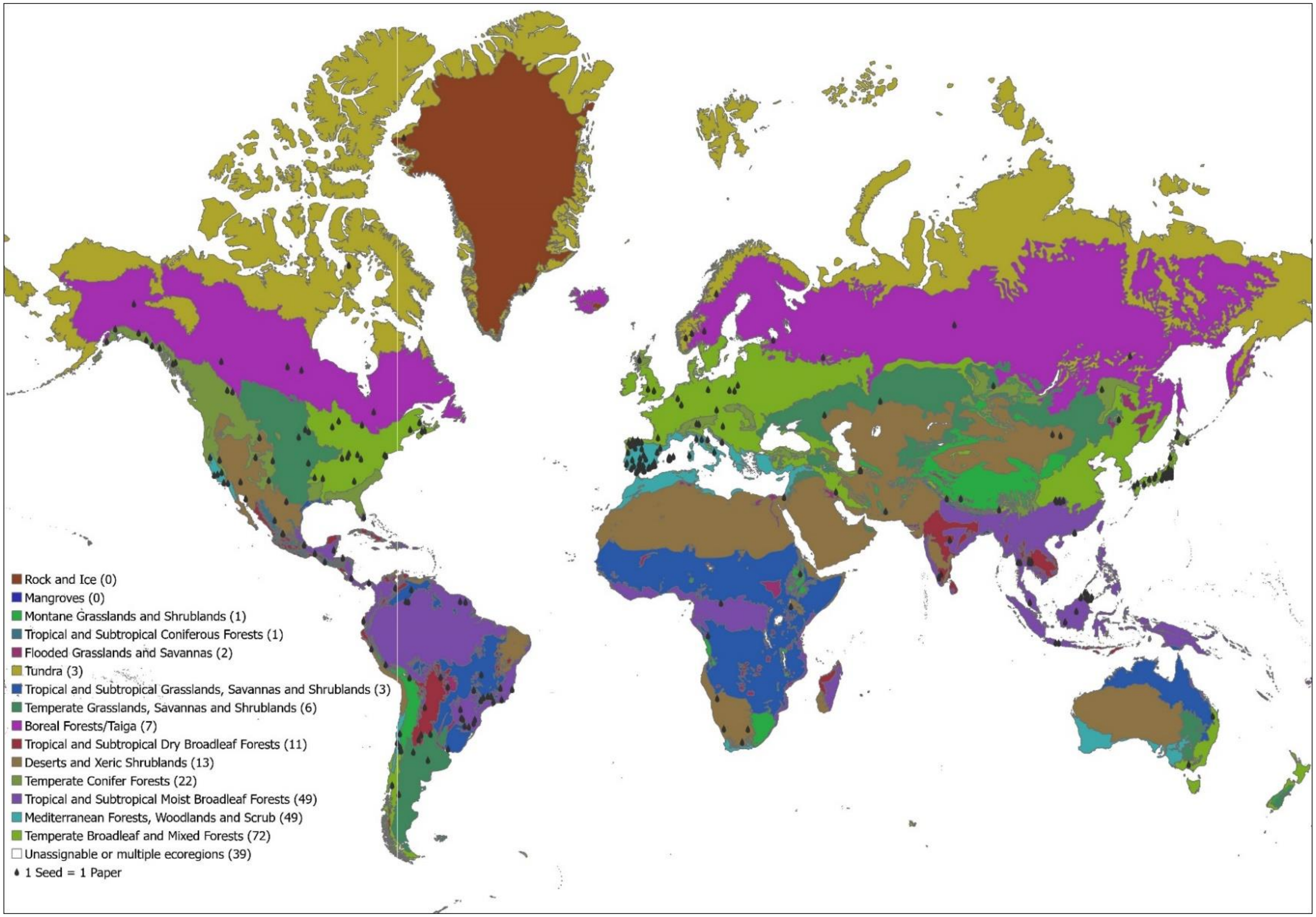
Rock and Ice (0)
Mangroves (0)
Montane Grasslands and Shrublands (1)
Tropical and Subtropical Coniferous Forests (1)
Flooded Grasslands and Savannas (2)
Tundra (3)
Tropical and Subtropical Grasslands, Savannas and Shrublands (3)
Temperate Grasslands, Savannas and Shrublands (6)
Boreal Forests/Taiga (7)
Tropical and Subtropical Dry Broadleaf Forests (11)
Deserts and Xeric Shrublands (13)
Temperate Conifer Forests (22)
Tropical and Subtropical Moist Broadleaf Forests (49)
Mediterranean Forests, Woodlands and Scrub (49)
Temperate Broadleaf and Mixed Forests (72)
☐ Unassignable or multiple ecoregions (39)
1 Seed = 1 Paper

Figure 2.1. We conducted a literature search as outlined in Box 2.1. The search yielded 280 peer-reviewed publications that observed or discussed *Carnivoran* consumption of fruit and seed. Each seed on this map represents a study that explored or discussed *Carnivoran* frugivory or seed dispersal. The map is divided by ecoregion as compiled by The Nature Conservancy (Wiken 1986, Bailey 1995, Olson and Dinerstein 2002), included in the legend is the total number of studies identified in that ecoregion. We were unable to assign 39 studies to a specific ecoregion as they addressed frugivory and seed dispersal at a wide spatial scale that crossed multiple ecoregions or used captive animal studies of species that crossed multiple ecoregions in their wild ranges.

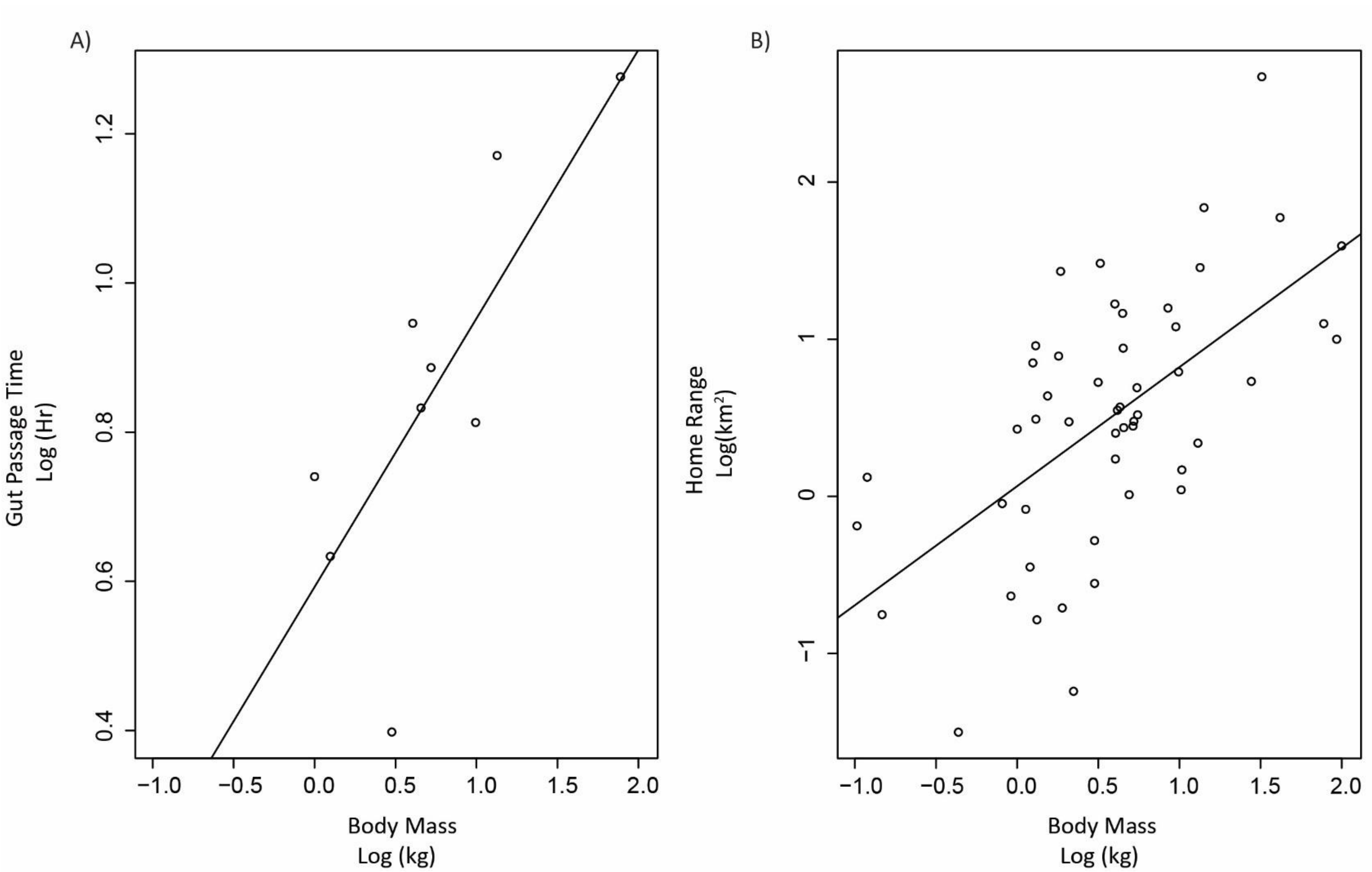

Figure 2.2. Relationships between gut passage time, home range, and body mass in *Carnivorians*. (A)Linear regression between the log body mass (kg) and log gut-passage time (hours) of 10 *Carnivoran* species (p-value =0.01, r-squared = 0.54). (B) Linear regression between the log mass (kg) and the log home range (km^2) of 51 *Carnivoran* species (p-value <0.001, r-squared value = 0.35). Gut-passage time, body mass, and home range values were derived from the available literature for species identified in our literature search as frugivorous *Carnivorans* (Appendix A: Supplemental Table 5).

Box 2.1. We carried out a literature search using search term pairs of frugivory or seed dispersal terms and various identifiers for *Carnivorans* including general terms (e.g. carnivore), common names, genus, and species names (Appendix A: Supplemental Table 2). The search was an exhaustive pairing of all combinations of frugivory and *Carnivoran* terms, carried out on the Scopus reference database during November of 2020. This returned a total of 1746 papers. The papers were then hand-curated to remove papers that were not peer-reviewed or were included due to a double meaning of the relevant search term, leaving 340 relevant papers. Next, papers were removed that did not involve frugivory including papers involving diplochory of the seeds within a prey item's stomach or seed predation such as the consumption of pine nuts or acorns. 278 papers met our complete search criteria (Appendix A: Supplemental Table 1).

Tables

Table 2.1. Breakdown of the distribution of studies we found in our literature search described in Box 2.1 by family and genus, and whether those studies looked at seed dispersal or frugivory in each taxonomic group. Publications that studied multiple genera or families are counted in this table as separate studies for each genus.

Family	Genus	Total Count	Count of Frugivory	Seed Dispersal
Canidae		**150**	**55**	**95**
	Atelocynus	1		1
	Canis	26	10	16
	Cerdocyon	9	4	5
	Chrysocyon	3	2	1
	Cuon	1	1	
	Lycalopex	19	7	12
	Nyctereutes	14	9	5
	Otocyon	3		3
	Urocyon	10	4	6
	Vulpes	64	18	46
Mustelidae		**126**	**48**	**78**
	Eira	4	2	2
	Lutra	1	1	
	Martes	71	26	45
	Meles	36	14	22
	Melogale	3		3
	Mustela	9	5	4
	Neogale	1		1
	Neovison	1		1
Viverridae		**59**	**29**	**30**
	Not specified	1		1
	Arctictis	10	7	3
	Arctogalidia	2	2	
	Civettictis	3	1	2
	Cynogale	1	1	
	Genetta	6	2	4
	Hemigalus	1	1	
	Paguma	12	6	6
	Paradoxurus	13	5	8
	Prionodon	1	1	
	Viverra	4	2	2
	Viverricula	5	1	4

Table 2.1. (cont.)

Ursidae		**60**	**25**	**35**
	Not specified	1		1
	Helarctos	4	2	2
	Melursus	1		1
	Tremarctos	2	2	
	Ursus	52	21	31
Procyonidae		**46**	**28**	**18**
	Bassaricyon	1	1	
	Bassariscus	5	3	2
	Cerdocyon	1		1
	Nasua	14	8	6
	Potos	6	6	
	Procyon	19	10	9
Mephitidae		**4**	**3**	**1**
	Conepatus	2	1	1
	Mephitis	1	1	
	Spilogale	1	1	
Herpestidae		**2**	**0**	**2**
	Herpestes	2		2
Hyaenidae		**2**	**2**	**2**
	Hyaena	2	2	
Ailuridae		**1**	**1**	**0**
	Ailurus	1	1	
Nandiniidae		**1**	**1**	**0**
	Nandinia	1	1	

Table 2.2. Animal body mass, gut-passage time, and the range of gut-passage time of *Carnivoran* species identified as frugivores/seed dispersers. All values are for adults of both sexes unless noted otherwise. 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.

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

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

CHAPTER 3

MESOPREDATOR FRUGIVORY HAS NO EFFECT ON SEED VIABILITY AND EMERGENCE UNDER EXPERIMENTAL CONDITIONS[1]

Abstract

Members of the order *Carnivora* are unique and important seed dispersers that consume and deposit undamaged seeds while providing regular long-distance seed dispersal opportunities. Some members of *Carnivora*, such as coyotes (*Canis latrans*), are undergoing range expansions which may help the plant species they consume colonize new locations or replace dispersal services provided by recently extirpated species. In this study, we evaluated aspects of the seed dispersal effectiveness of coyotes and gut passage time to determine the potential dispersal distances for three commonly consumed and commonly occurring plant species (*Amelanchier alnifolia, Celtis ehrenbergiana*, and *Juniperus osteosperma*). We also investigated the potential effects of secondary dispersal of seeds away from scats by comparing seedling emergence from whole scats to those where seeds were first removed from scats. We found that seeds generally took between 4 and 24 hours to pass through the digestive tract of coyotes, which could result in regular seed dispersal up to 7 km. Gut passage through coyotes had no effect on seed viability or emergence for any of the three plant species, including that gut passage for *A. alniflia* and *J. osteosperma* does not replace cold stratification for breaking physiological dormancy. By simulating secondary dispersal, we found that 22% (± 8.2%) more *C. ehrenbergiana* seedlings emerged when seeds were removed from scats and those seedlings emerged 7 days earlier (± 5 days) compared to seeds that remained in the coyote scat. Coyotes are effective seed dispersers, with the potential for regular long-distance dispersal services and

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[1] Draper, J. P., T. B. Atwood, N. G. Beckman, K. M. Kettenring, and J. K. Young. 2021. Mesopredator frugivory has no effect on seed viability and emergence under experimental conditions. Ecosphere 12.

for providing opportunities for secondary seed dispersal, which could aid in climate migration or serve to replace extirpated dispersal mutualists.

Introduction

Seed dispersal is necessary for sexually reproducing plant species to maintain gene flow and recruitment within a population and for migration and gene flow among populations (Levin et al. 2003, Levine and Murrell 2003). Dispersal aids in maintaining both plant community diversity and within-species genetic diversity, thereby improving community and species stability and persistence (Clobert et al. 2012). Additionally, dispersal improves the survival of individual propagules by moving them away from intraspecific competition or inhibition (Grubb 1977, Schupp and Fuentes 1995), specialized pathogens, and from predators that are attracted to an abundance of seeds and propagules immediately surrounding a maternal plant (Janzen 1970, Connell 1971, Comita et al. 2014). Seed dispersal also allows for the colonization of unpredictable or newly available habitats (Howe and Smallwood 1982). Effective seed dispersal occurs when quality seed (i.e., undamaged and viable) is deposited in quality locations (i.e., safe sites suitable for germination and growth) in sufficient quantities to ensure population establishment (Schupp 1993, Schupp et al. 2010). Thus, many species have adapted to utilize animals to increase the quantity of seeds transported in short- and long-distance dispersal through various mutualisms and commensalisms (Levin et al. 2003). Understanding the efficacy of these dispersal strategies and their mutualist or commensalist relationships is crucial to understanding and modeling seed dispersal.

Endozoochory is a form of seed dispersal that occurs via a mutualistic relationship with a vertebrate whereby the seed is transported inside the animal's digestive tract post-consumption. In many cases, seeds are covered with edible, fleshy fruit that promotes consumption by animals, which increases the quantity of seeds dispersed. Seed treatment by endozoochoric dispersers (e.g., mechanical damage during mastication; damage during digestion) can vary between different disperser and plant species and is an important aspect of the quality of seed dispersal effectiveness (Schupp 1993, Schupp et al. 2010, Perea et al. 2013). If seeds are unharmed, fruit consumption allows seeds to germinate after gut passage and feces deposition (Cypher and Cypher 1999, Steyaert et al. 2019). In some endozoochoric relationships, animal consumption of seeds can improve seed germination by removing fruit pulp, scarifying seed coats, and breaking physiological seed dormancy including for species that might otherwise require cold stratification (Traveset et al. 2007, Soltani et al. 2018).

Despite their name, many members of the order *Carnivora* [e.g., bears (*Ursus sp*.) and foxes (*Vulpes sp.*)] are highly omnivorous and consume large volumes of fruit; therefore, providing substantial seed dispersal services (Rogers and Applegate 1983, Rosalino and Santos-Reis 2009, Lalleroni et al. 2017). The quantity and quality of seeds dispersed by *Carnivorans* make them a particularly important seed disperser in some regions. For example, *Carnivorans* in North America are considered the main mammalian seed disperser of all plant species (Willson 1993). Furthermore, *Carnivorans*' seed-laden scats are valuable resources for scatter-hoarding, secondary seed dispersers, such as granivorous rodents (Enders and Vander Wall 2012, Shakeri et al. 2018). *Carnivorans* are important seed dispersers not only because they consume and deposit a substantial quantity of viable seeds, but they also have relatively large home ranges that can result in the long-distance dispersal of seeds (González-Varo et al. 2013, Herrera et al. 2016, Lalleroni et al. 2017). Long-distance seed dispersal is important for plant ecology and conservation because it facilitates gene flow among populations and the colonization of new areas (Falk and Holsinger 1991).

Coyotes (*Canis latrans*) are mesocarnivores that occur throughout most of North America and consume a wide variety of fruits (Kitchen et al. 1999, Roehm and Moran 2013). The generalist diets of coyotes allow them to take advantage of different prey items as they become available, including several seasonal fruits (Morey et al. 2007, Petroelje et al. 2013). Seeds deposited in natural ecosystems from coyote frugivory commonly result in neutral or increased germination (Schupp et al. 1997, Roehm and Moran 2013). However, the effects on some seeds can be negative (Cypher and Cypher 1999). Because results are generally neutral or positive, coyotes are hypothesized to be effective seed dispersers for many plant species. However, no controlled studies have investigated the effects of gut passage or gut passage time on seed viability and germination. Such information would improve our understanding of coyotes as effective seed dispersers and our ability to model seed dispersal by coyotes.

Coyotes are an interesting seed disperser because, unlike many frugivores, their range is expanding. Since the 1950s, coyotes have expanded their range by 40%, the largest expansion of any North American *Carnivoran* in the same period (Laliberte and Ripple 2003, Hody and Kays 2018). In the early 1900s, coyotes primarily inhabited the unforested western two-thirds of North America. Today, coyotes are found in taiga, deciduous, coastal temperate, and tropical forests from Canada and southern Alaska to Central America (Hody and Kays 2018). Because coyotes disperse viable seeds, their range expansion could be aiding in broader dispersal and colonization patterns of the plant species they consume. Additionally, in areas where coyotes are recent arrivals, they could be supplementing or replacing dispersal services previously carried out by species whose numbers have been reduced or have been extirpated entirely (Pérez-Méndez et al. 2016), as has been seen with other non-native *Carnivoran* species (Celedón-Neghme et al. 2013, Muñoz-Gallego et al. 2019). However, before we can understand the significance of coyotes as seed dispersers, we must first understand three key aspects of seed-coyote interactions: gut passage time (which influences how far a seed can be dispersed), its effect on seed viability, the rate and timing of germination, and the potential quantity of viable seeds dispersed.

This study had five main goals: 1) We measured gut passage time for three plant species (*Amelanchier alnifolia, Celtis ehrenbergiana*, and *Juniperus osteosperma*) from genera commonly consumed by coyotes (Schupp et al. 1997, Cypher and Cypher 1999, Dumond et al. 2001, Schrecengost et al. 2008). 2) We examined how gut passage through a coyote affects seed viability and seedling emergence of *A. alnifolia, C. ehrenbergiana,* and *J. osteosperma.* 3) We examined how diet composition may alter viability and emergence of *A. alnifolia, C. ehrenbergiana,* and *J. osteosperma*. 4) We also determined if gut passage could break physiological seed dormancy for the two plant species in this study with physiological seed dormancy (which is often broken by cold stratification and sometimes scarification, A. alnifolia, and J. osteosperma). 5) Finally, we experimentally evaluated the potential effect of secondary dispersal on quantitative and qualitative components of seed dispersal effectiveness. The results of this study are important for understanding the role coyotes play in seed dispersal.

Methods

Seed selection

We identified 16 genera of plants with seed-bearing bodies consumed by coyotes (Schupp et al. 1997, Cypher and Cypher 1999, Dumond et al. 2001, Schrecengost et al. 2008). Three genera were identified that had distributions spanning the conterminous United States, were common within their respective geographic ranges, and had a subordinate species that were available from seed distributors or wild collection: Saskatoon serviceberry (*A. alnifolia,* 4-10 seeds per pome), desert hackberry (*C. ehrenbergiana,* 1 seed per drupe), and Utah juniper (*J. osteosperma,* 1-2 seeds per dry cone). *Celtis ehrenbergiana* and *J. osteosperma* both typically require cold stratification to break physiological seed dormancy (Baskin and Baskin 2014), allowing us to test if coyote gut passage could replace cold stratification in breaking dormancy. All three genera are woody taxa with wide spatial distributions (USDA and NRCS 2020), and at least *Juniperus* is already experiencing range expansion (Weisberg et al. 2007, Rowland et al. 2011), making them interesting models for evaluating *Carnivoran* consumption and dispersal potential. *Amelanchier alnifolia* and *C. ehrenbergiana* were both purchased as whole dried fruits from native seed distributors (Native Seed Company and Granite Seed, respectively). In contrast, *J. osteosperma* seed cones were collected from a wild population in Green Canyon near Logan, Utah, USA. Before feeding, the *A. alnifolia* and *C. ehrenbergiana* fruits were rehydrated to ensure consumption by coyotes and to emulate wild presentation.

Captive coyote trials and gut passage time

Captive coyotes housed at the USDA - National Wildlife Research Center's Predator Research Facility in Millville, Utah, USA were fed 650 g of a high-protein, high-fat commercial food (Fur Breeders Agricultural Cooperative, Logan, Utah, USA) daily and provided water *ad libitum*. Coyote feeding trials took place between 20 June 2019 and 25 Nov 2019 and involved 20 coyotes. All coyotes were housed as male-female pairs in either 1,000 or 10,000 m^2 outdoor enclosures but are regularly fed in a fixed location of equivalent size within each enclosure. Experimental feedings for this study included three diet ratio treatments: a control feeding (650 g of regular food), one-third seed-bearing body (217 g of fruit/cone and 433 g regular food, ~2,170 *A. alnifolia* fruits, 1,670 *C. ehrenbergiana* fruits, and 800 *J. osteosperma* cones), and two-thirds seed-bearing body (433 g fruit/cone and 217 g regular food, ~4,330 *A. alnifolia* fruits, 3,330 *C. ehrenbergiana* fruits, and 1,600 *J. osteosperma* cones) for each of the three plant species. Two different proportions of seed-bearing bodies in feedings were used to determine if diet composition altered gut-passage time (Cipollini and Levey 1997) and the effect of gut passage on seed viability and germination due to differences in digestion with an increase in plant matter (Auger et al. 2002). We fed all coyotes their regular diet for a minimum of two days between experimental feedings. Each experimental feeding was mixed with a non-toxic glitter to allow for the identification of target scat after deposition (Burns et al. 1995). Although coyotes were housed as mated pairs, we fed them separately, and their food was mixed with different colors of glitter to enable the identification of scats to the individual. Twelve coyotes were fed for each treatment. Failure to participate occurred when a coyote refused to consume the experimental feeding or the coyotes ate from both feeding stations preventing individual ID of the resulting scats. All successful participants were observed until feeding concluded (feeding generally lasted 2-7 minutes) to establish gut passage start times. After each experimental feeding, the enclosure was checked after 4, 8, 24, and 48 hours to establish gut-passage time. All scats were collected and air-dried at room temperature to prevent mold formation before seed viability testing and emergence trials. All feeding trials were conducted under approval from NWRC's Institutional Animal Care and Use Committee (QA-3051).

Post-consumption seed viability testing

We blocked scats into groups by species of seed, the proportion of seed-bearing bodies in feeding, individual coyote, and time interval collected for viability tests post-consumption (Figure 3.1). Scat was randomly selected from each block for seed viability testing if multiple scats were collected. The seeds were removed from each scat using water and by progressively sieving the scat with a starting mesh of 6.35 mm and a finishing mesh of 2.12 mm. If a scat failed to yield 100 seeds, it was discarded, and another one was randomly selected. This method was used for both *C. ehrenbergiana* and *A. alnifolia*. No single scat yielded more than 50 *J. osteosperma* seeds; therefore, multiple scats from within the same block were randomly selected and combined to yield 100 seeds. To establish baseline seed viability, we tested three control samples of 100 seeds from the purchased *C. ehrenbergiana* and *A. alnifolia* seed lots and six control samples of 100 seeds from the wild-collected *J. osteosperma* due to its higher variability in viability. We followed the guidelines in the AOSA/SCST Tetrazolium Testing Handbook for seed viability tests (AOSA 2010). After being cut to expose the embryo, seeds were soaked for 18 hours in a 1% tetrazolium solution at ~ 30° C. Then, the exposed embryo was inspected for the intensity of staining as relevant for each species (AOSA 2010).

Post-consumption seedling emergence testing

We randomly selected a scat from each block for seed emergence trials in a common garden experiment. Each selected scat was divided in half; seeds were removed from one half as described above in the seed viability testing and the other half remained intact in the scat. Controls consisted of 100 seeds each for *C. ehrenbergiana* and *A. alnifolia*. A half scat from the *J. osteosperma* trials yielded approximately 25 seeds each and their seeds are quite large; thus, the controls were limited to 25 seeds so that the germination conditions were similar (e.g. seed density, distance from the soil surface, and vertical arrangement with other seeds) between the control and removal experimental samples. Removed seeds, intact scats with seeds, and controls were planted in a research greenhouse at Utah State University in Logan, Utah, USA. Whole scats were placed on the surface of the potting soil to replicate natural deposition, while removed seeds and control seeds were covered with potting soil to simulate scatter-hoarding (Beck and Vander Wall 2010) and optimal germination conditions, respectively (Bonner et al. 2008). The greenhouse was maintained at 21^{o} C, a temperature common in germination guidelines for all three species (Bonner et al. 2008, Beck and Vander Wall 2010). Supplemental lighting was provided to maintain a 12-hour photoperiod. Samples were kept moist and checked for new emergence every 36-72 hours. Emergence trials were run for 70 days (Bonner et al. 2008). The *A. alnifolia* and *J. osteosperma* seeds were not cold stratified to break seed dormancy (Bonner et al. 2008, Baskin and Baskin 2014) because we wanted to test whether or not gut passage would break dormancy as has been observed in other endozoochoric relationships (Traveset et al. 2007, Soltani et al. 2018).

Data analysis

We ran linear and mixed effect models to test the effect of gut-passage time and diet composition on seed viability, time to first emergence, and total number emerged while controlling for the variation in individual coyote gut-passage times. Gut passage time and diet composition were both treated as continuous variables, with the mid-point of each collection interval being used for gut passage time (2,6,16,36 hours respectively). We also ran mixed effect models to evaluate the effect of varying fruit concentrations in the diet (one-third seed-bearing body versus two-thirds seed-bearing) on gut-passage time. Finally, a pairwise t-test was run to compare days to first emergence and total emergence for removed seed samples and whole scats.

Results

Of the 20 individual coyotes used in this study, between 10 and 12 individuals successfully participated in five of the six treatment diet combinations: 12 participated in the treatment of one-third seed-bearing body for *J. osteosperma*, 11 participated in both diet ratio treatments for *A. alnifolia,* and the one-third seed-bearing body treatment for *C. ehrenbergiana*, while only 10 participated in the two-thirds seed-bearing treatment for *C. ehrenbergiana*. The two-thirds ratio treatment of *J. osteosperma* failed to yield sufficient participation and samples because only five coyotes consumed this combination.

Gut passage time

A total of 484 scats were collected, 6% between 0-4 hours, 20% between 4-8 hours, 61% between 8-24 hours, and 13% between 24-48 hours for all treatments and the control (Table

3.1). Inclusion of seed-bearing bodies in the diet, the seed species, and feeding proportion did not affect average gut passage time (Appendix B: Supplemental Table 1, 14.82 hours, n = 484, S.E.= 0.96). We did not detect a difference in gut passage time for individual coyotes (Appendix B: Supplemental Table 1).

Post-consumption seed viability

A total of 40 *A. alnifolia*, 27 *C. ehrenbergiana*, and 13 *J. osteosperma* samples consisting of 100 seeds each were tested for viability post-consumption (Table 3.1). Consumption and gut passage did not alter seed viability ratios compared to the control samples. An increase in the duration of gut passage (β=0.0, p=0.54) and diet ratios (β=0.04, p= 0.27) similarly showed no significant change in seed viability ratios (Figure 3.2, Appendix B: Supplemental Table 1).

Post-consumption seedling emergence

In total, 31 *A. alnifolia*, 22 *C. ehrenbergiana*, and 9 *J. osteosperma* samples were used for germination trials alongside three controls (un-digested seeds) of each species (Table 3.1). For all species, seedling emergence rates did not differ between the control and removed seed treatment. Seedling emergence was exceptionally low for the control and experimental treatments of *J. osteosperma* seeds (zero seeds emerged in control and experimental treatments) and *A. alnifolia* seeds (only one seed from an experimental treatment emerged and none from the controls), preventing further comparisons. The removed seed treatment, simulating secondary dispersal for *C. ehrenbergiana,* had a 22% ± 8.2% (95% CI) higher rate of emergence (p-value <0.001, n = 412/1765 of removed seeds; n = 136/2677 of seeds in whole scats emerged), and first emergence was 7 days earlier (± 5 days 95% CI, p-value = 0.009) compared to emergence from an intact scat. Diet ratio treatments and gut passage time did not affect the emergence ratio or the number of days to first emergence (p ≥ 0.1, Appendix B, Appendix B: Supplemental Table 1).

Discussion

Coyote range expansion and dietary breadth illustrate their potential for effective seed dispersal at both short and long distances. As coyotes expand their range, especially southward (Hody and Kays 2018), they are encountering an increasing number of fleshy fruited plants that have evolved for some level of endozoochory. Our results support the hypothesis that coyotes can act as effective seed dispersers for *Amelanchier*, *Celtis*, and *Juniperus* species. We found no indication that consumption by coyotes or gut passage time affects seed viability of the three plant species studied. However, gut passage did not appear to improve seedling emergence for any of the plant species, and gut passage was not effective at breaking dormancy for *A. alnifolia and J. osteosperma* seeds, which typically require cold stratification. We also found that removing seeds from coyote scat improved seedling emergence speed and rate for *C. ehrenbergiana*, suggesting that secondary dispersal by scatter-hoarders may increase the quality of seed dispersal services by coyotes.

Current coyote diet patterns suggest that coyotes will consume any available fruit and, in turn, disperse their seeds (Kitchen et al. 1999, Roehm and Moran 2013). The establishment of novel mutualistic relationships is important for seed dispersal for two reasons. First, long-distance or atypical dispersal may be needed to help plants disperse to new locations that have recently become suitable because of climate change or anthropogenic land-use change (Corlett and Westcott 2013). Second, new dispersers can compete with native disperses, or replace native dispersers that have been extirpated or are ecologically extinct (Celedón-Neghme et al. 2013, Pérez-Méndez et al. 2016, Muñoz-Gallego et al. 2019). If coyotes can play these roles, they may help maintain existing fruit-bearing plant populations by providing regular dispersal and genetic exchange or improving plant dispersal under changing climate conditions.

Amelanchier alnifolia, *C. ehrenbergiana*, and *J. osteosperma* seeds consumed by coyotes had average gut passage times between 4 and 24 hours, with the majority being deposited more than 8 hours post-consumption. Seeds that were deposited up to 48 hours post-consumption had no reduction in viability. Although the two species that require cold stratification never emerged, C. *ehrenbergiana* seeds had no reduction in total emergence for any gut passage duration. Coyotes can regularly travel 7 km or more in 24 hours (Young et al. 2006) and even average 0.94 km/hr of net displacement (Kitchen et al. 2000) within home ranges of between 10 and 16 km^2 (Chamberlain et al. 2000, Gosselink et al. 2003, Gifford et al. 2017). All of these factors combined suggest that coyotes can provide more regular long-distance dispersal opportunities than other sympatric seed dispersers that may offer more irregular but longer distance dispersal (Escribano-Avila et al. 2014).

Our results support that coyotes are qualitatively effective seed dispersers, as our results show no negative effects on seed viability or emergence for all gut-passage times and seed quantities. We were unable to test the qualitative effectiveness of deposition location in this study, but other studies have shown canids tend to deposit seeds in suitable locations for germination and recruitment (Escribano-Avila et al. 2014). As fairly prolific consumers of fruit (Kitchen et al. 1999, Roehm and Moran 2013), our findings also suggest coyotes are quantitatively effective seed dispersers. In this study, every consumption resulted in the deposition of viable seeds, even after extended gut-passage times or high seed volume feedings. However, gut passage did not appear to improve seedling emergence for any of the plant species studied.

Two of the plant species used in this study, *A. alnfolia* and *J. osteosperma*, typically require cold stratification to break dormancy (Baskin and Baskin 2014). Plants dependent on cold stratification are particularly vulnerable in the face of climate change due to the additional niche requirement of sustained cold temperatures before germination (Poschlod et al. 2011). Previous studies have suggested that gut passage can aid in dormancy break for such species (Traveset et al. 2007, Soltani et al. 2018), making them less vulnerable to warming climates without needing to migrate as far from their current range. Our results found that coyote gut passage alone was not sufficient to break dormancy for either plant species. Thus, although coyotes may deposit viable seeds at farther distances than some other frugivores, our results suggest suitable habitats at the deposition site would still need to have prolonged cold periods to stimulate germination for these plant species. Thus, coyotes' long-distance dispersal services could be valuable for climate migration, but they do not appear to assist with local climate adaptation for *A. alnfolia* and *J. osteosperma*.

The quality of coyote seed dispersal improved when seeds were removed from scats by improving seedling emergence speed and rate. Seeds removed from scats had a 22% higher rate of emergence, suggesting that the scat's physical or chemical structure inhibited viable seeds from emerging. Additionally, large numbers of seeds deposited as a single scat may reduce seed dispersal quality due to inherent competition between seedlings if they are not spread out before emergence. Rodents regularly forage from the concentrated seed resource available in *Carnivoran* scats (Shakeri et al. 2018). The seeds collected by granivorous rodents are either immediately consumed, larder hoarded, or scatter hoarded (Beck and Vander Wall 2010). Consumption inherently reduces dispersal quality and quantity, and larder hoarding deposits seeds too deep for effective emergence, reducing dispersal quality (Beck and Vander Wall 2010). However, scatter-hoarding deposits seeds in many different locations (increasing the quantity and diversity of dispersal locations) at depths that are more conducive to germination and emergence (Beck and Vander Wall 2010), essentially acting as gardeners planting seeds (increasing the quality of dispersal). Scatter hoarding is also the most common fate for seeds collected by granivorous rodents (Beck and Vander Wall 2010, Barga and Vander Wall 2013). Thus, secondary seed dispersal may improve the quality of coyote seed dispersal by increasing the quantity of dispersal locations from one to many, and the quality of seed fate (increased emergence) in those locations. However, further studies examining the interplay between coyote seed consumption and secondary dispersers are needed.

Intraspecific variation of both the plant being dispersed and the dispersal mutualist is important to understand seed dispersal dynamics fully. Variation in plant characteristics including, fecundity, fruit, and crop size, can affect the qualitative and quantitative aspects of endozoochoric dispersal due to the quality of the seed itself or its attractiveness and availability for a high quantity of consumption (Schupp et al. 2019, Snell et al. 2019). Variation in disperser dominance, sex, behavior, and body size affect their access to seeds, travel distance during gut passage, and volume of seeds consumed (Zwolak 2018). This study utilized homogenized seed lots and controlled both feeding volume and access to the food in captive coyotes. Thus, using a highly controlled experimental population of coyotes limits any inferences we could make regarding intraspecific variation in gut-passage time (which we did not detect) and its implications for potential dispersal distance. However, the controlled nature of this study allowed us to examine the effects of diet composition and gut passage time on seed viability and germination, which would have been very challenging to study using a wild population of coyotes.

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Tables

Table 3.1. The number of scats collected at each collection interval for each seed volume treatment and the control diet feeding, the number of samples from each treatment block, and control used in both tetrazolium testing (viability) and germination testing. For tetrazolium testing a sample was delineated by a single scat from its respective block for *Amelanchier alnifolia* and *Celtis ehrenbergiana* seeds and as a combination of scats from within the same sampling block for *Juniperus osteosperma* to reach a 100 seed sample size. All germination testing samples were single scats with varying volumes of seeds contained therein. The two-thirds ratio of *J. osteosperma* and the 0-4 hour interval for all treatments failed to yield sufficient samples for viability and germination testing, and the *Juniperus* control required additional replicates due to higher variability in viability.

	One-third volume					**Two-thirds volume**						
Time interval	**0-4 hours**	**4-8 hours**	**8-24 hours**	**24-48 hours**	**Total**	**0-4 hours**	**4-8 hours**	**8-24 hours**	**24-48 hours**	**Total**	**Control**	
Scat collection											10	**0-4 hours**
A. alnifolia	3	8	71	6	88	3	21	45	19	88	29	**4-8 hours**
C. ehrenbergiana	2	9	37	6	54	5	19	24	7	55	60	**8-24 hours**
J. osteosperma	6	13	52	13	84	--	--	--	--	--	16	**24-48 hours**
Total	11	30	160	25	226	8	40	69	26	143	115	
Viability testing												
A. alnifolia	--	5	10	3	18	--	8	11	3	22	3	
C. ehrenbergiana	--	1	9	1	11	--	7	7	2	16	3	
J. osteosperma	--	1	10	2	13	--	--	--	--	--	6	
Total	--	7	29	6	42	--	15	18	5	38	12	
Germination testing												
A. alnifolia	--	2	11	--	13	--	5	10	--	15	3	
C. ehrenbergiana	--	1	9	--	10	--	4	5	--	9	3	
J. osteosperma	--	1	6	2	9	--	--	--	--	--	3	
Total	--	4	26	2	32	--	9	15		24	9	

Figures

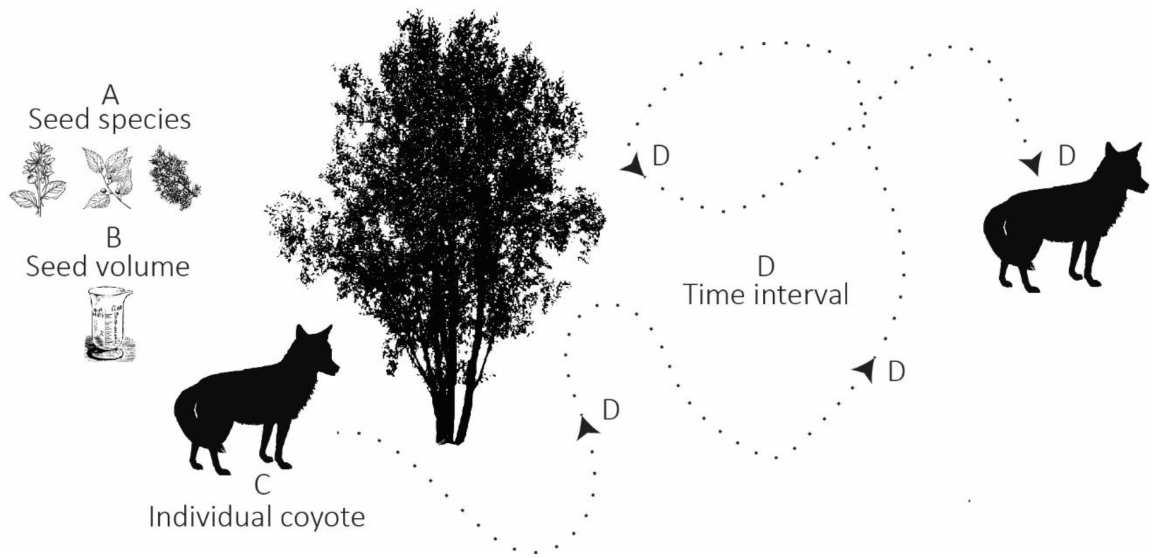

Figure 3.1. Experimental design. Scat samples from captive coyotes fed seed-bearing bodies of three different plant species (*Amelanchier alnifolia, Celtis ehrenbergiana*, and *Juniperus osteosperma*) were blocked for post-consumption viability and emergence testing first by seed species (A) to detect any variation in species tolerance for gut passage, then by the proportion of the fruits/cones in the feeding by mass (B) to evaluate if diet composition altered the effect of gut passage on seeds. Next samples were blocked by the individual coyote (C) to control for pseudoreplication and to detect any individual variation. Finally, samples were blocked by the post-consumption time interval (D) that they were collected to determine if longer gut passage times and thus longer dispersal distances had an effect on seed viability or emergence.

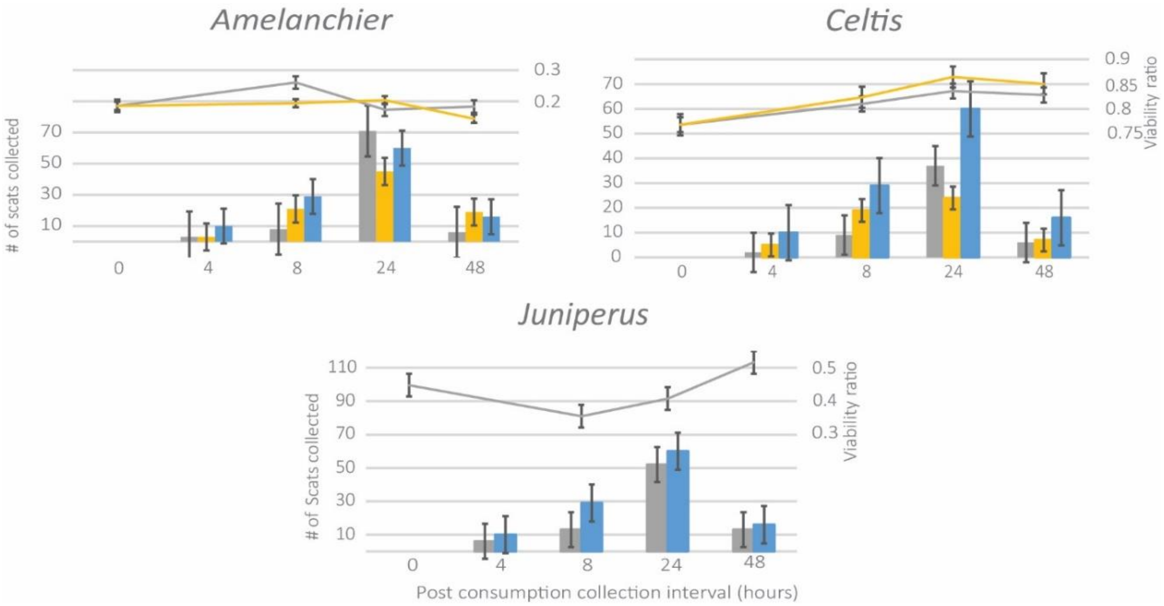

Figure 3.2. Seed viability ratios. Captive coyotes were fed standardized feeding treatments consisting of a mixture of their regular diet of a high-protein, high-fat commercial food, and 1/3rd and 2/3rd seed-bearing bodies by mass, of three plant genera that their wild counterparts commonly consume (*Amelanchier alnifolia (a), Celtis ehrenbergiana (b)*, and *Juniperus osteosperma (c)*). Gut passage duration had no significant effect on seed viability for any of the species, nor did feeding composition for *A. alnifolia* or *C. ehrenbergiana* seeds (the 2/3rd *J. osteosperma* treatment failed to yield sufficient samples for testing). All values are the mean of each treatment block with standard error bars around them.

CHAPTER 4

THE DIFFERENTIAL CONTRIBUTION OF COYOTES AND PASSERINES ON FUTURE BIOTIC CARBON STORAGE THROUGH JUNIPER SEED DISPERSAL[1]

Abstract

Differences in seed dispersal distances and patterns can alter plant distributions, species survival, plant community composition, and biotic carbon maintained and added to the landscape. Though *Carnivorans* are known to be frugivorous, their contribution to seed dispersal is marginally studied especially compared to other sympatric dispersers such as passerines. In this study, we evaluated how coyote (*Canis latrans*) seed dispersal differed from passerine (*Passeriformes*) seed dispersal for juniper (*Juniperus*) in the coterminous United States under future climate change. We modeled changes in juniper niche suitability starting in 2021 through the next 80 years of climate change by estimating the current niche with Maxent then using climate predictions to define spatial changes in suitable niches. Seed dispersal was simulated by both dispersers to estimate total juniper dispersal, juniper encroachment into grasslands, and finally changes in above-ground biotic carbon storage due to juniper encroachment. My results indicate that over the next 80 years, suitable conditions for juniper will contract, but losses from the current range will be minimal. Coyote dispersal of juniper will result in a 54-59% increase in range, which is 2.5 times as much as provided by passerines. Additionally, coyotes will facilitate juniper encroachment into 170,000-185,000 km^2 of current grasslands, 3.4 times as much as passerines. Coyote-mediated juniper encroachment of grasslands will provide between 1.1 and 1.2 Pg of carbon storage with the addition of woody aboveground biomass. Coyotes and passerines provide very different outcomes for changes in juniper ranges, plant community composition, and landscape carbon storage. Understanding the differences in outcomes

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[1] Co-authored with Julie K Young, Trisha B Atwood and Noelle Beckman

provided by different seed dispersers is important for modeling plant species distributions and carbon storage, as vertebrate ranges and abundances change altering local dispersal guilds.

Introduction

Seed dispersal is a crucial life stage for plants, and how plants are dispersed across a landscape influences individual plant recruitment, plant community composition and fitness, and ecosystem functioning (Levin et al., 2003). Seed dispersal away from a parent plant and conspecifics generally increases individual survival by reducing conspecific competition and inhibition, and by providing an escape from specialized predators, parasites, and pathogens that exist around an established population (Comita et al., 2014; Connell, 1971; Janzen, 1970). Increasing dispersal distance also improves the connectivity of disjunct patches and populations, which can improve genetic diversity and resiliency to changing conditions (Bohrer et al., 2005; Risson, 2012). The effectiveness of dispersal and the cascading effects it has on plant recruitment and plant community composition can ultimately impact ecosystem functioning, such as landscape-level biotic carbon storage (Bello et al., 2015).

Plants have evolved multiple mechanisms to facilitate seed dispersal and, in some cases, maximize dispersal distance, including structures surrounding and adjacent to seeds that optimize wind, water, and animal dispersal vectors (Levin et al., 2003). To maximize one form of animal-assisted seed dispersal, called endozoochory, plants provide fruit to attract animal consumption of seeds, which are dispersed when regurgitated or defecated (Harper 1977). Endozoochory aids in seed dispersal away from the plant where the fruit was consumed, improving seedling establishment and population connectivity, and can increase the potential for the seedling to locate rare or patchy resources necessary for recruitment (i.e. directed dispersal, Grubb 1977, Higginbotham 1993, Hohning-Gaese 2007). Endozoochory provides effective seed dispersal by dispersing a large quantity of quality seeds broadly across a landscape (sensu Schupp et al. 2010).

Birds and mammals provide important endozoochoric seed dispersal services. Within these classes, passerines (*Passeriformes*) and carnivores (*Carnivora*), respectively, are particularly important seed dispersers in North America (Stiles, 2000; Willson, 1993). Species within both vertebrate groups aid the plant species they disperse by removing the pulp and scarifying seeds (Traveset et al., 2007), but they differ in regards to dispersal distance and deposition location (Escribano-Avila et al., 2014). Passerines tend to consume seeds and disperse them within a contiguous forest or brushy patch with ample perches and available fruit (Herrera & García, 2010). Seeds are therefore deposited under the canopy of both hetero-specific and conspecific plant species near where the fruit was consumed (Bartuszevige & Gorchov, 2006; Chavez-Ramirez & Slack, 1994). Conversely, carnivores tend to deposit seeds at greater distances from where they were consumed and in more varied habitats, including open habitats, closed canopies, and along habitat edges of travel corridors (Escribano-Avila et al., 2014; González-Varo et al., 2013; Rubalcava-Castillo et al., 2020; Suárez-Esteban et al., 2013). The longer travel distance often observed in carnivore seed dispersal may increase connectivity with more distant conspecific plant populations and allow plants to colonize new areas or locate suitable regeneration conditions that may be rare or patchy on the landscape (Fedriani et al., 2018; Rost et al., 2012), but may also result in dispersal away from suitable conditions.

Climate change is altering the spatial distribution of the ecological niche (suitable conditions necessary for survival and reproduction) of many plant species, which can result in range shifts, (e.g. contractions and expansions; Lenoir and Svenning 2015). Changes in climate conditions relevant to a plant's ecological niche will force plants to either adapt or migrate to follow suitable conditions, while those that cannot employ either strategy will go extinct.

Effective seed dispersal (*sensu* Schupp et al. 2010) helps to maintain genetic diversity within plant populations from the smallest patch to the entire species distribution (Higginbotham, 1993; Levine & Murrell, 2003), which in turn can facilitate adaption to perturbations in the climate (Kremer et al., 2012). Alternatively, effective seed dispersal can allow plants to track the leading edge of a range shift or even expand their range if climate change releases them from current constraints (Corlett & Westcott, 2013). Both *in situ* adaptation and migration benefit from the efficacy and dispersal distance provided by different seed dispersal partners, making understanding the differences in dispersal vectors or partners important to understanding future plant community distributions.

Carnivores have been documented consuming and dispersing 115 different plant genera in North America, and one of these carnivores, the coyote (*Canis latrans*), consumes at least 50 of them (Chapter 1). In addition to coyotes being a prolific fruit- and seed-consuming species, their range has expanded over 40% in the last 70 years and continues to expand today (Hody & Kays, 2018). This range expansion has created new seed dispersal mutualisms (Roehm & Moran, 2013), providing an interesting comparison to studies that focused on the effect of defaunation on seed dispersal and biotic carbon storage (Bello et al., 2015; Culot et al., 2017; Peres et al., 2016). One plant commonly consumed and dispersed by coyotes and several species of passerines is juniper (*Juniperus,* Schupp et al. 1997, Chambers et al. 1999). Juniper dispersal is important to study because junipers are encroaching on historic grasslands in North America due in part to increased susceptibility of grasslands to conversion caused by livestock grazing and changes in fire regimes (Filippelli et al., 2020). This encroachment alters critical habitat for threatened and endangered species (Caracciolo et al., 2017; Coates et al., 2017; Van Auken, 2009). The invasion of grasslands by woody plants like junipers can cause changes in the environmental services provided by grasslands (Barger et al., 2011), including significant increases in above-ground carbon storage through their wood structures (Fernandez et al., 2013; Throop & Lajtha, 2018).

In this study, we modeled the changes in future above-ground biotic carbon storage based on different endozoochoric seed dispersal vectors. To predict how a changing environment will affect different woody species of juniper, we first predicted future maximum distributions of multiple juniper species, then determined how different seed dispersal mutualists affected juniper exploitation of these future distributions. We utilized coyotes as the model species representing carnivores due to their prolific range expansion covering the entire conterminous United States (Hody & Kays, 2018), generalist diets (Lendrum, 2017), and known consumption of juniper fruits (Chambers et al., 1999; Schupp et al., 1997). Additionally, coyote consumption of juniper seeds and subsequent gut passage has no negative effect on seed viability (Draper et al., 2021). For comparison, we selected a representative community of passerines with well-documented consumption of juniper fruits and large contiguous ranges that co-occur with coyote and juniper (Chambers et al., 1999; A. M.A. Holthuijzen & Sharik, 1985; Stricklan et al., 2020). The passerine assemblage included American robin (*Turdus migratorius*), cedar waxwing (*Bombycilla cedrorum*), and European starling (*Sturnus vulgaris* (Chambers et al., 1999; A. M.A. Holthuijzen & Sharik, 1985; Stricklan et al., 2020). These species are also wide-ranging and not experiencing population declines (Sauer et al., 2014). We quantified how different patterns of dispersal between coyotes and these passerines would affect overall range expansion of junipers, grassland conversion to juniper, and the resulting differences in potential above-ground carbon storage. Results from this study illuminate the influence and importance that changes in the seed dispersal community can have on plant community composition and potential landscape-carbon stocks in aboveground biomass.

Methods

For our study, we focus on the dispersal of seeds from seven species of juniper (*J. californica, J. deppeana, J. monosperma*, *J. occidentalis, J. osteosperma*, *J. scopulorm,* and *J. virginiana*) by three passerines and coyotes across the conterminous United States. We selected the *Juniperus* genera of trees as our model plant because their fruits are regularly consumed by passerines and coyotes, they have large well-documented distributions, and are woody plants that have been encroaching on grasslands, with the potential to lead to significant changes in above-ground biotic carbon storage.

Four main data inputs were required to model the effect of different seed dispersal agents on aboveground biotic carbon storage: (1) species presence data for juniper species*,* (2) climate projections to define future conditions, (3) estimates of seed dispersal distances for avian species and coyote*s*, and (4) estimates of above-ground carbon storage in living biomass for both grasslands and juniper, which we then used to calculate the change in above-ground carbon storage for the conversion of grasslands to juniper as a result of dispersal by coyotes and passerines.

Seed Dispersers

We considered seed dispersal by a representative assemblage of passerines (American robin, cedar waxwing, and the European starling) considered to be the most prolific avian consumers of juniper (Chambers et al., 1999; A. M.A. Holthuijzen & Sharik, 1985). Observed dispersal by passerines showed an average dispersal between 12 and 40 m for junipers (Chavez-Ramirez & Slack, 1994; A. M.A. Holthuijzen & Sharik, 1985). Regular dispersal distances for passerines may range further based on gut passage time (~12- 30 minutes; Holthuijzen and Adkisson 1984, Bartuszevige and Gorchov 2006); however, post-consumption behavior and digestion by birds suggest that it is unlikely for them to disperse juniper seeds beyond a kilometer (Chambers et al., 1999; Chavez-Ramirez & Slack, 1994; Herrera & García, 2010; A. M.A. Holthuijzen & Sharik, 1985). Therefore, we estimated that average passerine seed dispersal would be limited to 1 km within suitable habitats that were immediately adjacent to established populations of juniper.

Coyote gut passage time while consuming *J. osteosperma* averages between 8 and 24 hrs (Draper et al. 2021). Coyotes can move on average ~0.94 km/hr (Kitchen et al., 2000) with a total displacement of 5.5 to 7 km over 24 hrs (Chamberlain et al., 2021; Young et al., 2006). However, much of a coyote's movement is constrained to its home range which can average between 10.6 and 20.7 km^2 for resident coyotes and over 200 km^2 for transients (Chamberlain et al., 2021; Gifford et al., 2017). Therefore, we estimated an average maximum distance of 5-km away from an established population for coyote seed dispersal. Although coyote home range size varies across habitats, we used this average across all habitat types to accommodate for computational limitations because it represents a fairly conservative maximum dispersal distance.

Dispersed plants

We obtained presence-only data for seven juniper species (*J. californica, J. deppeana, J. monosperma*, *J. occidentalis, J. osteosperma*, *J. scopulorum,* and *J. virginiana*) from the United States Forest Service Forest Inventory and Analysis National Program (Forest Inventory and Analysis, 2007). We utilized publicly available fuzzed and swapped data because it has been shown to perform well at resolutions finer than the 2.5 km^2 resolution we used for our ecological niche model (Gibson et al., 2014). Juniper species containing fewer than 50 observations were removed to ensure robust model predictions (Hernandez et al., 2006). The seven juniper species used in this study predominantly occur from the eastern front of the Rocky Mountains to the west coast, with a single species (*J. viginiana*) occurring east of the great plains (Forest Inventory and Analysis, 2007). All seven species produce a dry cone between 5 and 12 mm (USDA & NRCS, 2020), which provides nourishment to passerine and coyote consumers who in general pass the seeds intact (Draper et al., 2021; Anthonie M. A. Holthuijzen & Adkisson, 1984).

Landscape and climate model inputs

Bioclimatic variables for current and future conditions were downloaded from WorldClim (Fick & Hijmans, 2017) utilizing the CanESM5.0.3 projection due to its low bias in surface temperature and precipitation predictions over North America (Swart et al., 2019). We selected the shared socioeconomic pathways (SSP) 2-4.5 and 5-8.5, which model moderate and extreme future climate change scenarios, respectively. A shapefile of current grasslands generated from the National Land Cover Database (Homer et al., 2015) was used to define landscapes vulnerable to juniper encroachment.

Ecological niche models for juniper

To prepare occurrence data for modeling, we generated a 100-km buffer surrounding each occurrence and merged within species to provide a spatially appropriate region from which to draw background points (Barbet-Massin et al., 2012; Merow et al., 2013; Phillips et al., 2017). The Maxent modeling framework was chosen to estimate niche suitability for junipers due to its ability to utilize presence-only data (Phillips et al., 2004, 2017). We ran an exploratory model to identify the most important bioclimatic variables for junipers (Phillips et al., 2017). Each species was modeled with 100 replicates and evaluated using a receiver operator curve. Maxent results were then projected into future climate scenarios, using downscaled data reported in 20-year increments calculated by Fick and Hijmans (2017) to accommodate modeling and computing memory limitations (2021-2040, 2041-2060, 2061-2080, and 2081-2100) and under two SSPs scenarios (2-4.5 and 5-8.5) for the full extent of the conterminous United States (Figure 4.1).

Model of animal-mediated dispersal of juniper

Differences in dispersal potential of junipers between coyotes and passerines were modeled using the MigClim package in R (Engler et al., 2012; Engler & Guisan, 2009; R Core Team, 2021). We drew current occurrence maps for each plant species using binary Maxent model predictions under current climate conditions constrained to the background buffers for each species. All cells identified in the current occurrence map were assumed to be stable mature stands. Maxent modeling provided habitat suitability maps with occurrence probabilities for each time-step and SSP for each species. Current agricultural, urban, and suburban land use was excluded from habitat suitability maps due to a low likelihood of juniper establishing and growing to maturity in such conditions (Homer et al., 2015). Initial maturity for newly colonized raster cells was set to 10 years and dispersal was modeled as only occurring on alternating years per juniper ecology (USDA & NRCS, 2020). All newly colonized cells were assumed to have sufficient recruitment from the colonizing event to allow for pollination and production of viable seeds when mature. We assumed all mature cells maintained a stable density and age structure throughout the model run unless the Maxent model predicted local extinction. Map resolution was increased to 1 km^2 to meet the modeling needs of the cellular automata employed in MigClim. Dispersal probability for 1 km was set to 1 for both species, while coyote seed dispersal probability reduced linearly for distances of 2-5 km (0.8, 0.6, 0.4, 0.2), following the general trend observed in other canids (González-Varo et al., 2013). Dispersal estimates did not account for potential dispersal patterns during annual migrations. However, a rare long-distance of between 10 km and 20 km, the range of maximum dispersal distances given for average gut passage times and travel speeds of our model dispersers was included (Draper et al., 2021;

Anthonie M. A. Holthuijzen & Adkisson, 1984). This dispersal was modeled with a probability of 0.01, to allow for its inclusion without obscuring the differences in primary dispersal due to migration model sensitivity to LDD Migration models were run 100 times for each plant x disperser x SSP combination through four 20-yr time steps between 2021 and 2100.

Carbon storage model

We evaluated the differential contribution the two dispersers could have on woody encroachment into grasslands and their impacts on above-ground biotic carbon storage. The area of the intersection of current grasslands and the modeled future juniper distribution was multiplied by the average change in above-ground biotic carbon storage (3.9^{-6} Pg increase, SE= 8.9-7 Pg C) calculated from Barger et al. (2011) for the conversion of grassland to a juniper forest. This estimate of gross addition of above-ground biotic carbon storage was calculated for disperser x SSP combination, along with the total of uncertainties accumulated from all modeling steps. This estimate only accounted for the addition of above-ground carbon storage from grassland conversion and excluded possible changes due to loss of juniper stands or conversion of other habitat types. Below-ground biotic and abiotic carbon storage was excluded from this analysis due to complex interactions with soil type and soil microbe communities, and difficulties in estimating the diversity of root structures involved.

Results

The bioclimatic variables with the highest variable importance as estimated by the preliminary Maxent run for juniper presence were the highest temperature of the warmest month, annual precipitation, and precipitation during the warmest quarter of the year. Junipers favored warm climates with both lower annual and warm-season rainfall (Appendix C;

Supplemental Figure 1). The area under the curve for the receiver operator curves for the resulting Maxent models ranged between 0.80 and 0.94.

Current highly suitable climate conditions for juniper extend well beyond the current observed and predicted ranges. Juniper favors warm conditions during the warmest month of the year, and modest to low annual and warmest quarter precipitation. Under future climate scenarios, highly suitable conditions appear to be more tightly spatially aligned with the current predicted range of juniper (Figure 4.2). As the climate warms, suitable conditions advance upslope following a band of warmest month max temperature roughly between 20 and 35 degrees. However, this upward progress is limited in high-elevation areas where annual and warmest quarter precipitation remains high. Climate suitability is reduced in low-lying areas as conditions warm but is generally maintained within the existing juniper range. Three juniper species showed some contraction from their current range, with *J. deppeana*, *J. monosperma,* and *J. scopalorum* having modest losses of their original ranges under SSP 2-4.5 (> 1%). Under SSP 5-8.5 *J. deppeana*, and *J. scopalorum* lost < 5% of their original range, while *J. monosperma* lost 26.25% of its original range between 2081 and 2100. These range losses were predominantly in the lowland southern portion of its range, pointing to the presence of a ceiling for heat tolerance in juniper.

Under future climate conditions, both seed dispersers expanded juniper ranges, offsetting any losses caused by climate change. Under SSP 2-4.5 junipers expanded between 24% and 59% of their total range and under SSP 5-8.5, they expanded between 21% and 54% of their total. All range losses were offset by dispersal to areas with suitable niches by either seed disperser. Despite the large loss of original range for *J. monosperma* under SSP 5-8.5, this species expanded its total range by 21% to 46% by 2100. Dispersal for all species was greatest in regions where existing juniper populations abutted foothills, mountain ranges, and high plains, where they were able to constantly exploit suitable conditions (i.e. following suitable temperatures upslope, or exploit xeric conditions without extreme temperature increases) throughout the 80 years of our model.

Migration modeling showed that coyotes consistently provided 2.5 times greater range expansion for junipers compared to passerines (Figure 4.3, Appendix C: Supplemental Table 1). The difference in dispersal between the two taxa was more pronounced for grassland conversion, where coyotes provided 3.4 times more conversion than their passerine counterparts (Appendix C: Supplemental Table 2). For SSP 2-4.5, coyotes converted over 185,000 km^2 of grasslands to juniper woodlands while passerines converted less than 55,000 km^2. We found a similar trend between the two dispersers at SSP 5-8.5, albeit with less overall grassland conversion due to climate conditions being less suitable for juniper expansion (170,000 km^2 and ~49,000 km^2 of grassland converted for coyote and passerines respectively). The greatest amount of grassland conversion for both dispersers took place where juniper populations met with the Great Plains, particularly the northern portion.

Both coyote and avian dispersal aided in juniper encroachment of current grasslands leading to increases in landscape-level carbon storage. However, coyote-aided seed dispersal resulted in 0.85 Pg C (0.36 ± 0.08 vs 1.2 ± 0.3 Pg C) more carbon storage on the landscape by 2100 under SSP 2-4.5 compared to when junipers were only dispersed by passerine species (Appendix C: Supplemental Table 3). Similarly, coyote-aided seed dispersal under SSP 5-8.5 resulted in 0.76 Pg C (0.32 ± 0.08 vs 1.1 ± 0.27 Pg C) more carbon storage on the landscape by 2100 compared to passerines. Predictably, the three juniper species with the largest current ranges (*J. scopalorum, J. osteosperma,* and *J. occidentalis*) provided the largest contribution to grassland encroachment and increases in landscape-level carbon storage. *J. scopalorum* provided the most grassland conversion under all climate and dispersal scenarios, with encroachment largely occurring on the Great Plains and High Plains. *Juniperus osteosperma* and *J. occidentalis* convert more disjunct and higher elevation grassland areas, such as those in the Rocky Mountains, eastern Sierra Nevada Mountains, and the Sky Islands of the Great Basin.

Discussion

The differences in seed dispersal services provided by different dispersers within a guild have profound effects on plant migration, genetic diversity, species survival, and ecosystem function (Levin et al., 2003; Peres et al., 2016). The distribution, composition, and populations of different dispersal guilds are changing, with the distribution of some members contracting due to factors such as overhunting and other guilds having new members introduced through range expansion (Hody & Kays, 2018; Peres et al., 2016). To better predict plant species distributions in the future, we must understand how changes in the distribution of different seed dispersers are likely to affect different plant species. We found that a longer distance disperser like a coyote can provide 2.5 times as much range expansion for a woody plant than a passerine disperser group that distributes seeds closer to the source. These larger range expansions of seeds resulted in greater plant community conversion from grasslands to juniper woodlands, and in turn, resulted in greater above-ground biotic carbon storage. Our study exemplifies the importance of understanding different disperser's contributions to total seed dispersal changes (Rogers et al., 2019), and their cascading effects on plant species distribution, plant community composition, and landscape-level carbon storage.

Seed dispersal by both coyotes and passerines help all seven expand their range in the face of climate change. Juniper saw minimal losses of their existing range along the trailing edge of their distribution. These results bolster findings that juniper species are projected to be resilient to changing climate conditions (Volder et al., 2013), and will exploit higher elevations in response to warming (Guida et al., 2019). Future increases in temperatures at higher elevations allowed for maximum dispersal of juniper upslope and into high plains by coyotes in early timesteps, which in turn tapered off through time as climate change reduced suitable niches (Figure 4.3). Passerines on the other hand provided a constant rate of dispersal, never outpacing the change in niches. Both dispersers allowed junipers to track the leading edge of newly suitable areas and to compensate for losses at the trailing edge when they occurred.

The effect of the longer seed dispersal distances provided by coyotes vs. passerines is particularly pronounced where juniper is encroaching on grasslands. Current grasslands generally exist in climate niches suitable for juniper and remain suitable through 2100. This niche suitability allows juniper encroachment to exploit the full dispersal capabilities of coyotes from 2021 through 2100. As a result, coyotes can convert 3.4 times (>185,000 km^2 vs <55,000 km^2, at SSP 2-4.5) more area of grassland than passerines. Elsewhere dispersal was limited by the availability of newly suitable areas for juniper to expand into, resulting in a narrower difference in total range expansion with coyotes providing only 2.5 times more dispersal than passerines (970,000 km^2 vs 389,000 km^2 at SSP 2-4.5). Previous work has shown upwards of a four-fold increase in juniper range over 80 years (Rowland et al., 2011) and a 2% annual rate of grassland encroachment (Sankey et al., 2010). Our model found a maximum of a 1.6-fold increase over 80 years, and a maximum annual rate of encroachment of ~3,000 km^2 or 0.2% of total available grasslands. Comparison of these numbers is difficult as previous work has generally focused on more discrete ranges or ecosystems, while we focused on gross totals for the entire conterminous United States. Our lower rates of increase and encroachment are at least in part due to studying the entire range of juniper, rather than just a region currently experiencing high rates of expansion and encroachment. Additionally, though all grasslands were considered vulnerable to encroachment in our model, some were beyond the theoretical maximum dispersal potential of either disperser (but not beyond the long-distance dispersal parameter and thus kept in the model). The even lower rates of expansion and annual encroachment (1.24 and 794 km^2 or 0.05% respectively) provided by passerines under the same conditions suggest that juniper is dispersed by multiple unique seed dispersers that provide a range of dispersal distances; otherwise, the previously observed rates of expansion would not be possible.

Our results show that juniper will continue to encroach into grasslands under both moderate and severe climate change scenarios, provided that a vertebrate seed disperser persists as well. This encroachment will have a cascade of effects on the carbon storage capacity of the encroached landscape. Our model shows that future juniper encroachment will increase above-ground biotic carbon storage by 0.32 to 1.2 Pg C. Under both climate scenarios, coyote dispersal of juniper increases above-ground biotic carbon storage by more than three times as much as passerines, highlighting the magnitude of difference that the introduction or removal of a seed disperser can have on the carbon cycle (Figure 4.4). Juniper encroachment into grasslands also increases the volume and proportion of biotic carbon deposited on the soil surface as liter that is resistant to decay (recalcitrant), due to the higher lignin content in the woody parts of juniper (Norris et al., 2001). As a result of more recalcitrant carbon, this litter is then incorporated into both the duff layer and the soil as soil organic carbon (McKinley & Blair, 2008; Throop & Lajtha, 2018). A recalcitrant duff layer and increased soil organic carbon reduces the overall turnover of the accumulated biotic organic carbon, reducing both the magnitude and rate of soil carbon remineralization to CO_2. Thus, the conversion of grasslands to woodlands by vertebrate seed dispersers has the potential to increase the long-term storage capacity of carbon on the landscape.

Contrary to the positive results for carbon storage, increased woody encroachment of grass and shrublands can harm plant and wildlife communities. Juniper encroachment can reduce plant community diversity and richness (Ratajczak et al., 2012), which in turn can reduce a plant community or landscape’s overall resilience to disturbance (Chillo et al., 2011). Reducing the diversity of plant species also reduces the availability of forage by excluding more nutritive grasses and replacing them with largely unpalatable juniper leaves (Van Auken, 2009). Greater sage grouse (*Centrocercus urophasianus*), a vulnerable species in the Intermountain West, are particularly susceptible to the ill effects of juniper encroachment, as it not only reduces forage for sage grouse but also suitable lek sites that are crucial to their reproduction (Coates et al., 2017). Ultimately the landscape effects of juniper encroachment are mixed with positive outcomes for biotic carbon storage and potentially negative outcomes for plant diversity and conservation of vulnerable vertebrate species that require large intact grasslands.

Our model has a few limitations due to uncertainties. First, juniper is a heavily managed plant, and juniper encroachment into grasslands and other habitats is controlled through removal programs (Bombaci & Pejchar, 2016; Farzan et al., 2015). Historical removals of juniper could have reduced the diversity of climate conditions represented in our occurrence data, thus constraining their future suitable niche. Additionally, our model does not account for future management actions that may remove junipers and reduce their rate of expansion and encroachment. Finally, both grazing and fire are common occurrences in juniper habitats and grasslands. However, we did not account for the potential interactive effects that grazing and fire could have on landscape susceptibility to encroachment (Caracciolo et al., 2017) and carbon storage in aboveground biomass (Rau et al., 2012). Future research adding parameters accounting for fire and management actions would further improve the quality of this model to predict the future expansion of juniper and their overall effects on the landscape.

Several studies have focused on the negative effects that the loss of large-bodied, vertebrate seed dispersers have on plant dispersal, plant community composition, and carbon storage (Bello et al., 2015; Harrison et al., 2013; Pérez-Méndez et al., 2016). Our study is unique because we focused on how the expanding population and distributions of a vertebrate species, the coyote, across the USA may aid in juniper persistence and expansion under climate change. Our findings show that a diverse dispersal guild was important for helping junipers expand under moderate and severe climate change (Chanthorn et al., 2019; Peres et al., 2016). Longer distance seed dispersal provided by larger vertebrates, such as coyotes, was especially important for maintaining or increasing a plant's ability to track newly suitable climate conditions. In the case of juniper, dispersal by vertebrates into new areas helped offset any losses caused by the loss of suitable habitat from climate change. Not only did dispersal by vertebrates help juniper expand under climate change, but it also influenced the ability to convert grasslands to woodland, which ultimately increased landscape-level carbon storage. Our findings do not offer a solution or a direct management suggestion regarding the species studied. Rather we illustrate the importance of maintaining diverse seed dispersal guilds to help ensure that plant species and communities can meet new challenges caused by climate change with a robust natural response, and the importance of including *Carnivorans* in plant dispersal models.

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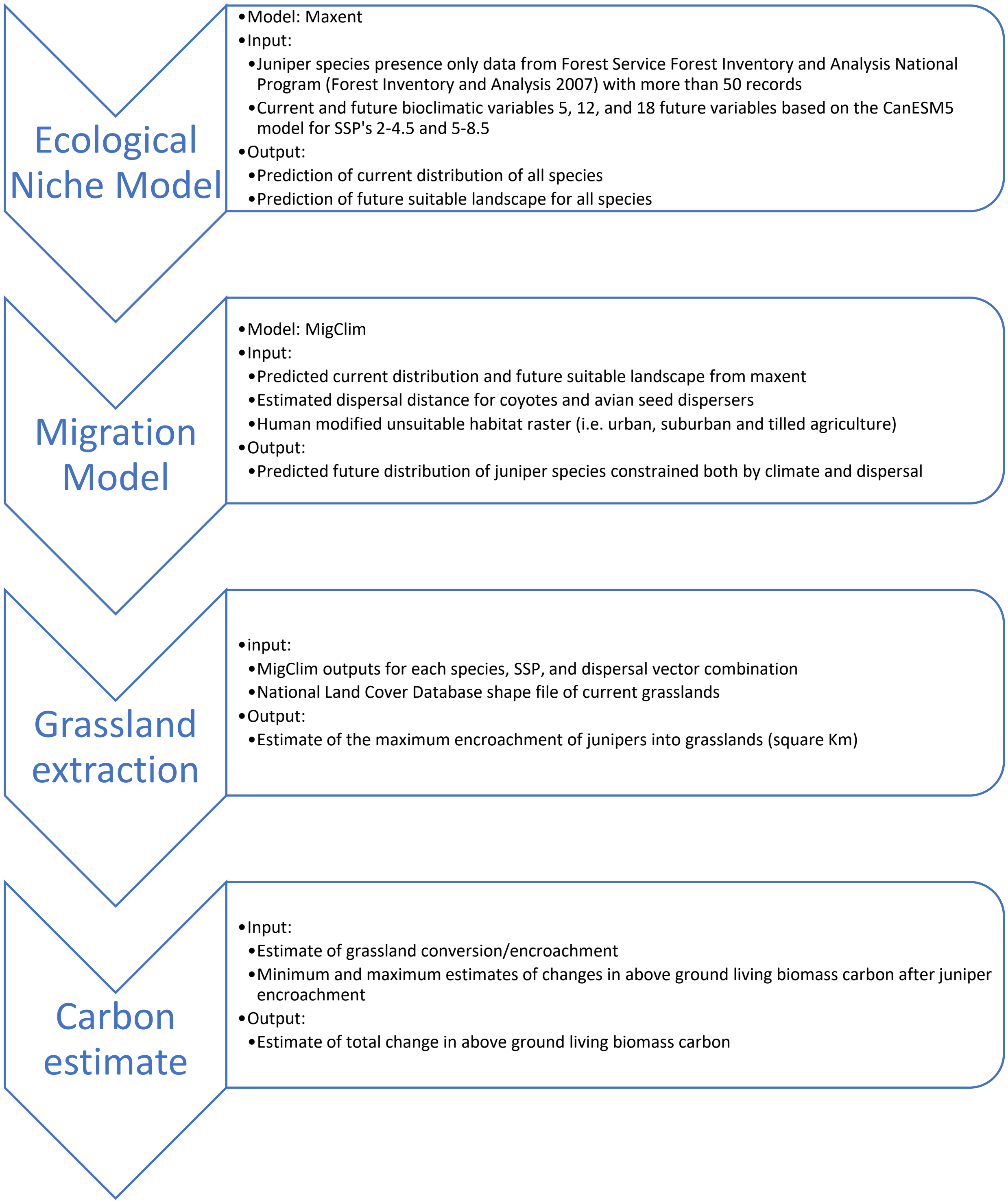
Figures



Ecological Niche Model

- Model: Maxent
- Input:
  - Juniper species presence only data from Forest Service Forest Inventory and Analysis National Program (Forest Inventory and Analysis 2007) with more than 50 records
  - Current and future bioclimatic variables 5, 12, and 18 future variables based on the CanESM5 model for SSP's 2-4.5 and 5-8.5
- Output:
  - Prediction of current distribution of all species
  - Prediction of future suitable landscape for all species

Migration Model

- Model: MigClim
- Input:
  - Predicted current distribution and future suitable landscape from maxent
  - Estimated dispersal distance for coyotes and avian seed dispersers
  - Human modified unsuitable habitat raster (i.e. urban, suburban and tilled agriculture)
- Output:
  - Predicted future distribution of juniper species constrained both by climate and dispersal

Grassland extraction

- input:
  - MigClim outputs for each species, SSP, and dispersal vector combination
  - National Land Cover Database shape file of current grasslands
- Output:
  - Estimate of the maximum encroachment of junipers into grasslands (square Km)

Carbon estimate

- Input:
  - Estimate of grassland conversion/encroachment
  - Minimum and maximum estimates of changes in above ground living biomass carbon after juniper encroachment
- Output:
  - Estimate of total change in above ground living biomass carbon

Figure 4.1. Flow chart of inputs and outputs of each modeling step in our analysis of juniper dispersal by two vertebrate seed dispersers, and the resulting rate of grassland encroachment and increases in above-ground biotic carbon storage under changing climate conditions.

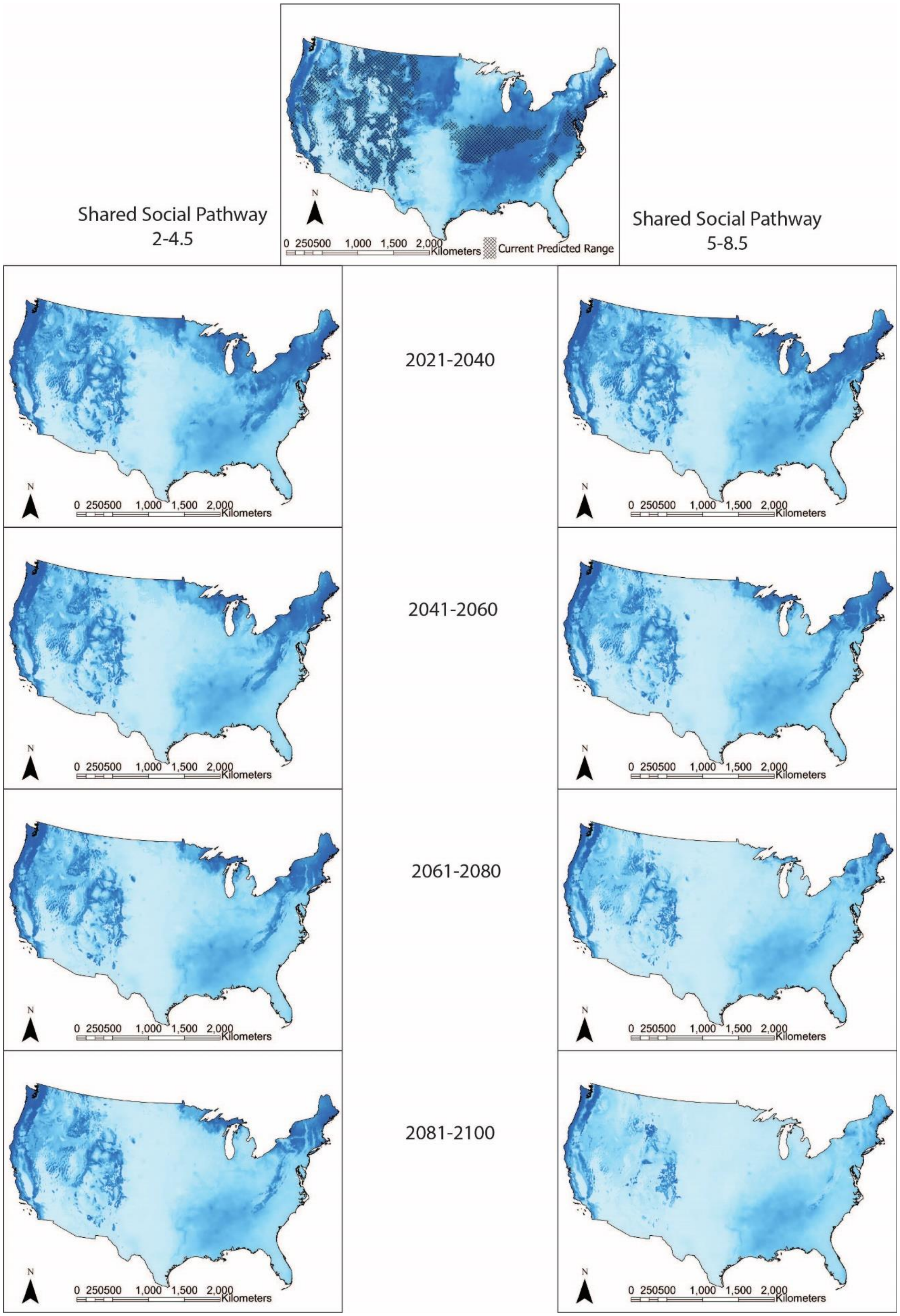
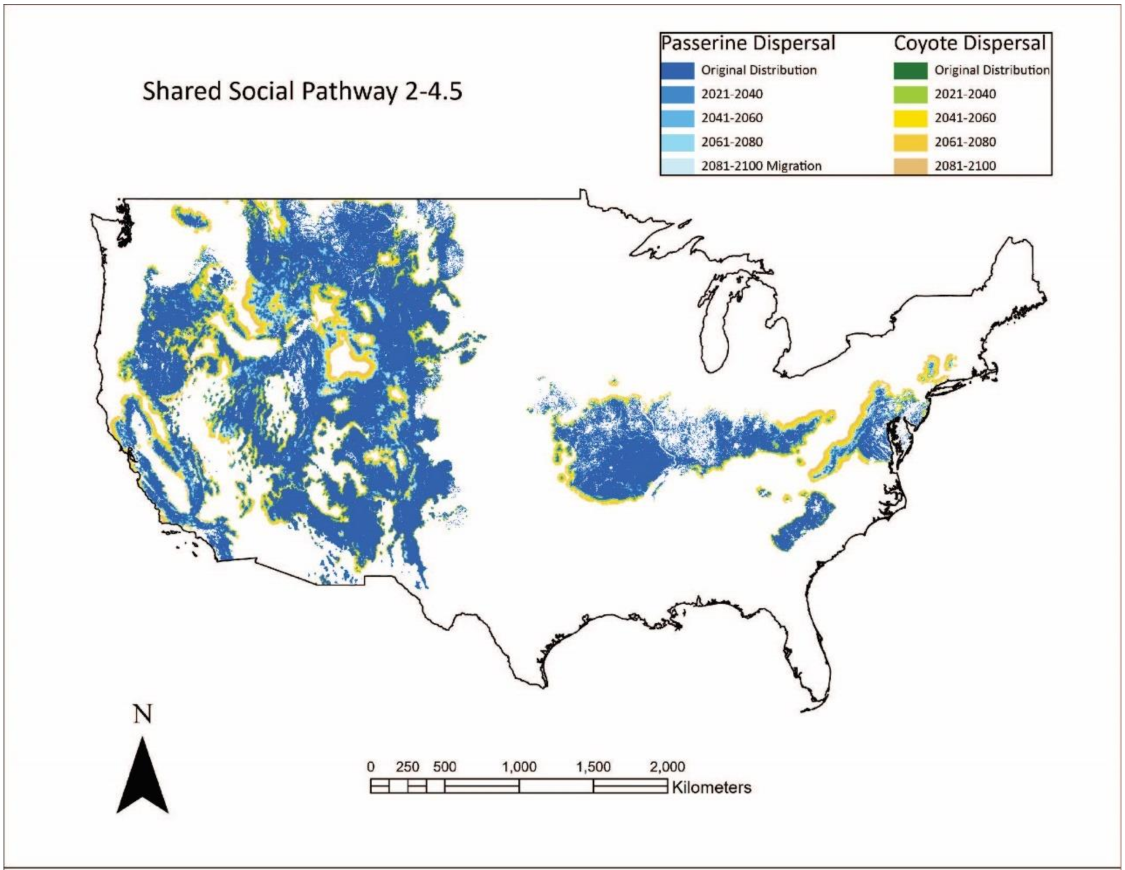

Shared Social Pathway 2-4.5
Shared Social Pathway 5-8.5
N
0 250500 1,000 1,500 2,000 Kilometers
Current Predicted Range
2021-2040
2041-2060
2061-2080
2081-2100

Figure 4.2. Ecological niche model results for seven species of juniper (*J. californica, J. deppeana, J. monosperma*, *J. occidentalis, J. Osteosperma*, *J. scopulorm,* and *J. virginiana*), under two different climate change scenarios (SSP 2-4.5 and 5-8.5). The top map represents the currently predicted suitability with darker blue representing increasingly suitable conditions. The cross-hatched areas represent the currently predicted occurrence of juniper in the conterminous United States. The eight lower maps represent the predicted suitability for juniper under the two climate change scenarios, across four future time steps. Suitability for juniper advanced upslope and north tracking favorable temperatures, and away from mesic conditions due to narrow precipitation tolerances.


Shared Social Pathway 2-4.5
Passerine Dispersal
Original Distribution
2021-2040
2041-2060
2061-2080
2081-2100 Migration
Coyote Dispersal
Original Distribution
2021-2040
2041-2060
2061-2080
2081-2100
N
0 250 500 1,000 1,500 2,000
Kilometers

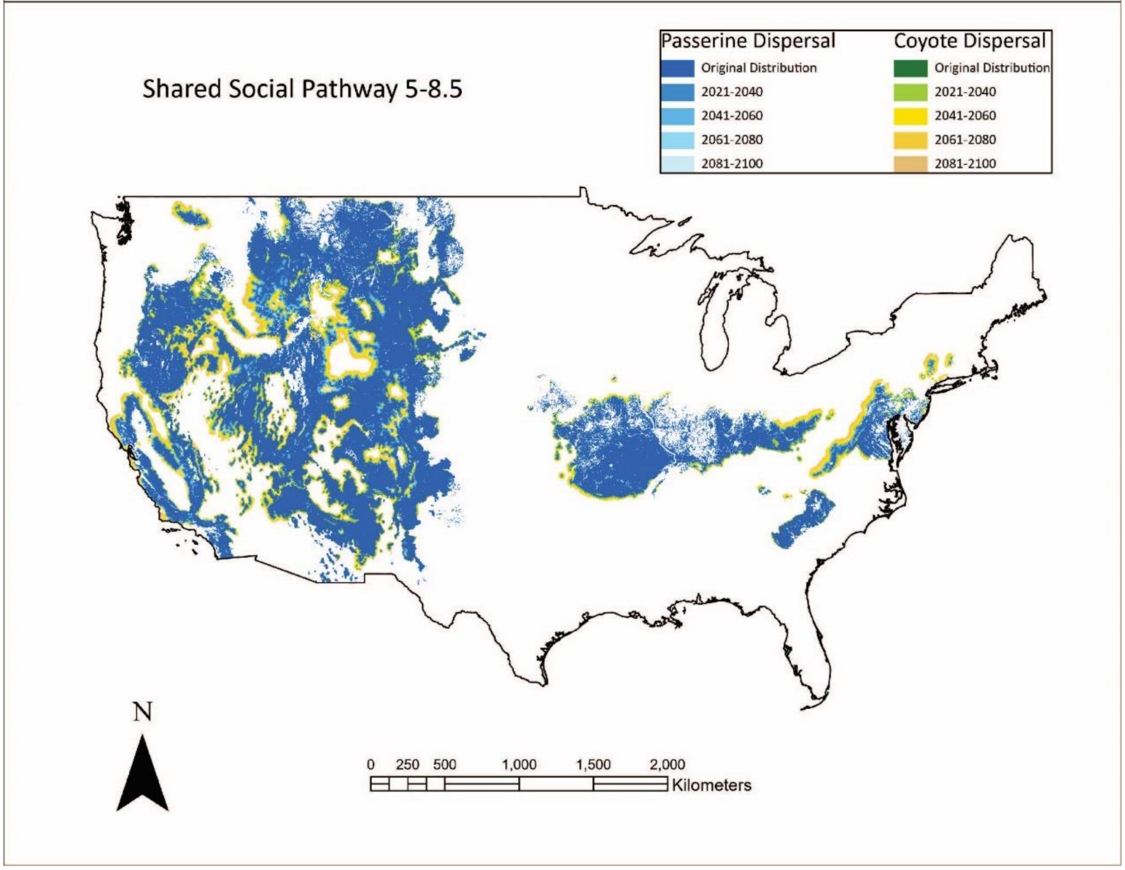

Shared Social Pathway 5-8.5
Passerine Dispersal
Original Distribution
2021-2040
2041-2060
2061-2080
2081-2100
Coyote Dispersal
Original Distribution
2021-2040
2041-2060
2061-2080
2081-2100
N
0 250 500 1,000 1,500 2,000
Kilometers

Figure 4.3. Juniper dispersal model results for dispersal by both coyotes (greens and yellows) and passerines (blues) across the conterminous United States from 2021-2100 under a moderate climate change scenario (Shared Social Pathway 2-4.5) and a severe climate change scenario (Shared Social Pathway 5-8.5). Passerine dispersal is displayed on top of the coyote dispersal; therefore all visible coyote dispersal is where it extends beyond the total dispersal provided by passerines throughout the entire 80-year model run. The dark blue represents the starting distribution of juniper for both species as the passerine original distribution directly overlays the coyote original distribution. Coyotes provide 2.5 times as much dispersal by 2100. The difference in dispersal between coyotes and passerines was highest at high elevation or where distributions abut mountain slopes where newly suitable conditions (hotter conditions during the warmest month) extended far enough ahead of the current distribution to make dispersal the primary mechanism.

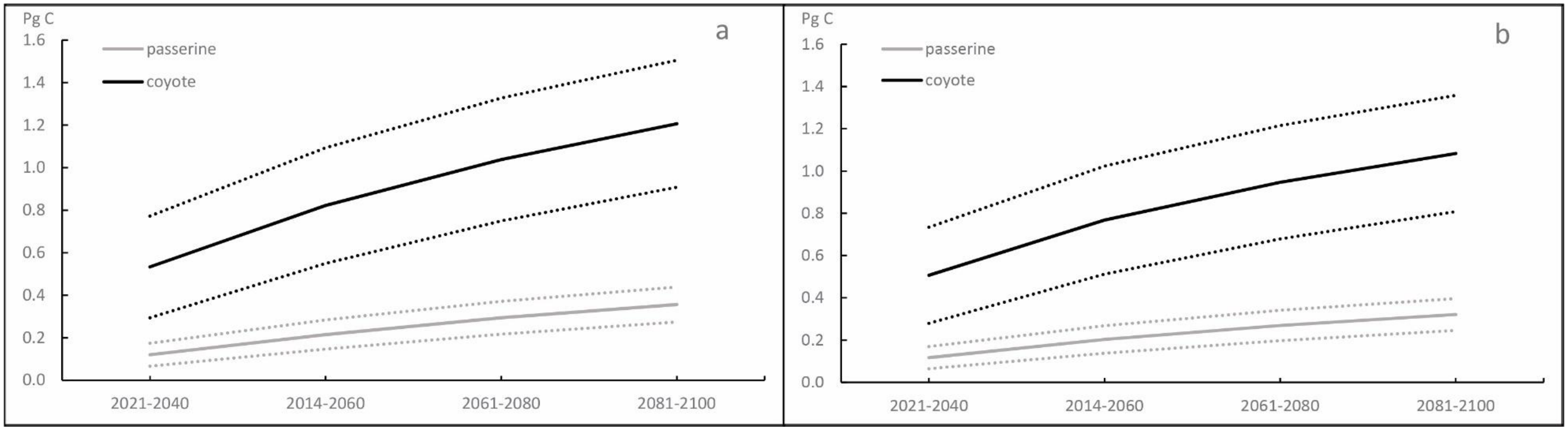


Figure 4.4. Gross new above-ground carbon storage provided by passerine and coyote mediated seed dispersal of junipers (*Juniperus sp.*) into grasslands. Values are reported in Petagrams of carbon (Pg C) with 95% confidence intervals that account for the cumulative error of all modeling steps

CHAPTER 5

CONCLUSION

The order *Carnivora* represents an important seed dispersal vector throughout the world because they disperse viable seeds to diverse locations a long distance from their source. This pattern aids in plant migration, plant community change, and changes in above-ground biotic carbon storage. I evaluated the current understanding of the prevalence of *Carnivoran* seed dispersal, its spatial and taxonomic breadth, and if *Carnivorans* are effective seed dispersers. I also explored the seed dispersal efficacy of a model Carnvioran species, the coyote, and determined gut passage time for fruit and seeds, seed viability and germination, and the effect of the proportion of fruit in the diet on these responses. Finally, I modeled the differential effect that a *Carnivoran* (coyote, *Canis latrans*), could have on seed dispersal, plant migration, woody encroachment, and carbon storage when compared to other sympatric seed dispersers under changing climate conditions.

In chapter 2, I found that effective seed dispersal is common within the order *Carnivora* both taxonomically and geographically. Ten out of the 13 terrestrial families in the order *Carnivora* are documented as being explicit seed dispersers or implicit seed dispersers based on the prevalence of frugivory. Frugivory in *Carnivora* was documented worldwide and across nearly all ecoregions. *Carnivorans* provide effective seed dispersal by depositing seeds in diverse and suitable locations for seed germination. Gut passage does not appear to hamper dispersals, as most seed-*Carnivoran* pairings result in the deposition of viable seeds, and only rarely result in suppressed germination. The current literature supports the hypothesis that *Carnivorans* are widespread effective seed dispersal.

The prevalence of *Carnivoran* frugivory is important for fruiting plant ecology because of the complementary nature of *Carnivoran* seed dispersal to other seed dispersers (Escribano-Avila et al. 2014). Given the diverse pairings of *Carnivorans* and plant species with positive outcomes for seed dispersal, *Carnivorans* are likely broadly augmenting seed dispersal and may be able to support plant species that are losing current seed mutualists (Chanthorn et al. 2019). Furthermore, *Carnivorans* may add a long-distance seed dispersal partner in areas where certain *Carnivorans* are expanding their range (e.g., coyotes; Hody and Kays 2018). The broad dispersal services *Canivorans* provide will help plant species maintain genetic diversity and migrate to adapt to escape climate change respectively (Kremer et al. 2012, Naoe et al. 2016).

My research highlights areas where more research on *Carnivoran* frugivory and seed dispersal is still needed to understand their contribution to seed dispersal. More studies on *Carnivoran* seed dispersal are particularly needed in Africa, Oceana, and western Asia. These three areas are home to many *Carnivoran* species that are within generas that have been identified elsewhere as seed dispersers, such as *Canis*, and Ursus (Roehm and Moran 2013, Lalleroni et al. 2017). Further research is needed in these locations to determine if patterns of dispersal capability are consistent or differ from their close relatives elsewhere. More research is also needed on the explicit spatial patterns of *Carnivoran* seed dispersal and seed dispersal effectiveness (SDE), as most studies attempting to estimate a dispersal kernel or SDE rely on inferences from gut passage time and post gut passage viability which does not account for the quality of the deposition location. Finally, further analysis should be done on the overarching pattern of effects that *Carnivoran* gut passage has on seed viability and germination either by plant family, seed morphology, or the *Carnivoran* who consumed them. Despite these gaps in knowledge, I was able to show that C*arnivorans* effectively disperse seeds worldwide.

In chapter 3, I found that coyotes have the potential to be effective seed dispersers. Coyote gut passage did not affect seed viability or germination rate, regardless of the length of gut passage time or diet composition. Coyote gut passage times averaged between 8 and 24 hours, providing the potential for regular long-distance seed dispersal. Finally, seed germination rate and speed were both suppressed when seeds remained impounded in scats, highlighting the importance of secondary dispersal from whole scats by scatter-hoarding granivores. Taken together my findings indicate that coyotes regularly disperse viable seeds long distances.

Coyote seed dispersal is of particular interest in the ecology of plants in North America because they are well-documented frugivorous *Carnivoran* (Cypher and Cypher 1999, Armenta-Méndez et al. 2020), and their range is rapidly expanding (Hody and Kays 2018). Coyotes have already shown a propensity to disperse novel seeds within their recently colonized range (Roehm and Moran 2013), making it likely that they will continue to establish new seed dispersal relationships with other fruiting species as they continue to expand their range. Coyotes also have a high tolerance for anthropogenic landscapes (Atwood et al. 2008), providing the opportunity for coyotes to disperse a variety of non-native plants from the urban and suburban landscape to surrounding wild spaces (Larson et al. 2020, Spennemann 2020). My findings support coyotes not only participating in these expanding seed dispersal roles but also that they are capable of providing effective seed dispersal at long distances.

Two limitations to my study provide opportunities for future research. First, logistical trade-offs prevented more frequent scat searches limiting a more fine-scale evaluation of gut passage time which would have provided a more nuanced look at potential dispersal distances and patterns. Second, only having two of three seed species germinate limited the inferences that could be made regarding germination vs viability post-consumption, and further exploration on the role gut passage plays in breaking seed dormancy. A new feeding study establishing a fine-scale estimate of gut passage time, paired with a field study mapping scat depositions on the landscape, could provide a model for fine-scale seed distribution. This model could also be validated using seed mimics in wild feeding trials. Another potential line of inquiry would utilize cold stratification to break seed dormancy of highly dormant species to evaluate the interplay of gut passage and dormancy break in a more detailed way. Chapter 3 provides a framework for which future studies, such as those suggested here or undertaken for different *Carnivorans*, could follow.

In chapter 4, I found that seed dispersers with different dispersal distances can provide different outcomes for plants under climate change and that these effects can cascade down to impact plant communities and carbon storage. Under changing climate conditions, juniper in the conterminous United States will disperse up-slope from their current distribution with minimal losses along the trailing edge of their distribution. Both passerines and coyotes disperse seeds into areas that are currently grasslands catalyzing woody encroachment and increasing above-ground biotic carbon storage. Under the same conditions, coyotes increased juniper ranges 2.5 times as much as passerines and provided 3.4 times as much encroachment. This difference in encroachment resulted in up to a 0.85 Pg of carbon storage difference between the different seed dispersers (0.36 vs 1.2 Pg C).

These findings show that understanding the total dispersal guild for a plant species is important for predicting the total dispersal kernel (Rogers et al. 2019). Differences in seed dispersal distance provided by different seed dispersers did not show a difference in the ability of juniper to survive climate change, but it did show a profound difference in range expansion and plant community conversion. These results are important because the overlooked group of seed dispersers in the order *Carnivora* are repatriating parts of their range (Sommer and

Benecke 2005, Draper et al. 2017), and coyotes specifically are drastically expanding across north and central America (Hody and Kays 2018).

This study's models were limited due to uncertainties surrounding previous and future land use management, and fire regimes. Previous management of juniper may have altered the occurrence records distorting the realized niche measured in the models, additionally, future management may result in the removal of newly dispersed juniper altering further dispersal and total dispersal, encroachment, and carbon storage estimates. Finally, my models did not account for the complex interplay of fire in these landscapes both in changing landscape susceptibility to encroachment or release of stored carbon after a juniper stand burns. Very naturally these limitations lead to possible future research to incorporate fire and management into predictions of juniper's future on the landscape, and the role that different seed dispersers may play. This research could be further extended by increasing the complexity of the model to include more species of plants and seed dispersers, as well as incorporating resistance values to landscapes that may be less susceptible to conversion. More research is needed to explore the varied and nuanced aspects of plant community distributions in the future as they are affected by climate, dispersal vectors, competition, and other factors.

This dissertation contributes to the general understanding of seed dispersal within the order *Carnivora.* My findings document the extensive nature of seed dispersal within a possibly improperly named order of animals and point to the likelihood that seed dispersal within the order *Carnivora* is much more widespread than currently documented. Furthermore, my findings show that individual species within *Carnivora* have the potential to provide extensive seed dispersal services altering landscapes and landscape-level biotic carbon storage.

References

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Larson, R. N., J. L. Brown, T. Karels, and S. P. D. Riley. 2020. Effects of urbanization on resource use and individual specialization in coyotes (*Canis latrans*) in southern California. PLoS ONE 15:1–23.

Naoe, S., I. Tayasu, Y. Sakai, T. Masaki, K. Kobayashi, A. Nakajima, Y. Sato, K. Yamazaki, H. Kiyokawa, and S. Koike. 2016. Mountain-climbing bears protect cherry species from global warming through vertical seed dispersal. Current Biology 26:R315–R316.

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APPENDICES

APPENDIX A. CHAPTER 2 SUPPLEMENTAL TABLES

Supplemental Table 1. Citations for all 280 studies that we found in this literature review, along with which *Carnivoran* families are discussed in each study and whether the focus of the study was on seed dispersal specifically or more generally discussed *Carnivoran* frugivory.

Citation	Family	Study Focus
Acevedo Quintero, J. F., and Zamora-Abrego, J. G. (2016). Role of Mammals on Seed Dispersal and Predation Processes of Mauritia Flexuosa (*Arecaceae*) In the Colombian Amazon. *Rev. Biol. Trop.* 64, 5. doi:10.15517/rbt.v64i1.18157.	Canidae	Seed Dispersal
Ackerson, B. K., and Harveson, L. A. (2006). Characteristics of a Ringtail (*Bassariscus astutus*) Population in Trans Pecos, Texas. *Texas J. Sci.* 58, 169–184.	Procyonidae	Frugivory
Adachi, T., Kuwahara, Y., and Takatsuki, S. (2016). A Long-Term Study of the Food Habits of the Japanese Marten in Northern Kyushu, Japan, With Reference to the Increased Population of Sika Deer. *原子力学会ー2016-1春* 4, 2016.	Mustelidae	Frugivory
Almeida, D., Copp, G. H., Masson, L., Miranda, R., Murai, M., and Sayer, C. D. (2012). Changes in the Diet of a Recovering Eurasian Otter Population Between the 1970s and 2010. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 22, 26–35. doi:10.1002/aqc.1241.	Mustelidae	Frugivory
de Almeida, A., Morris, R. J., Lewis, O. T., and Mikich, S. B. (2018). Complementary Roles of Two Resilient Neotropical Mammalian Seed Dispersers. *Acta Oecologica* 88, 9–18. doi:10.1016/j.actao.2018.02.011.	Procyonidae	Seed Dispersal
Alves-Costa, C. P., and Eterovick, P. C. (2007). Seed Dispersal Services by Coatis (*Nasua nasua, Procyonidae*) And Their Redundancy With Other Frugivores in Southeastern Brazil. *Acta Oecologica* 32, 77–92. doi:10.1016/j.actao.2007.03.001.	Procyonidae	Seed Dispersal
Alves-Costa, C. P., Da Fonseca, G. A. B., and Christófaro, C. (2004). Variation in the Diet of the Brown-Nosed Coati (*Nasua nasua*) In Southeastern Brazil. *J. Mammal.* 85, 478–482. doi:10.1644/1545-1542(2004)085<0478:VITDOT>2.0.CO;2.	Procyonidae	Frugivory
Amodeo, M. R., Vázquez, M. B., and Zalba, S. M. (2017). Generalist Dispersers Promote Germination of an Alien Fleshy-Fruited Tree Invading Natural Grasslands. *PLoS One* 12, 1–17. doi:10.1371/journal.pone.0172423.	Canidae	Seed Dispersal
Aragona, M., and Setz, E. Z. F. (2001). Diet of the Maned Wolf, *Chrysocyon brachyurus*, (*Mammalia: Canidae*), During Wet and Dry Seasons at Ibitipoca State Park, Brazil. *J. Zool.* 254, 131–136. doi:10.1017/S0952836901000620.	Canidae	Frugivory
Armenta-Méndez, L., Gallo-Reynoso, J. P., Wilder, B. T., Gardea, A. A., Ortega-Nieblas, M. M., and Barba-Acunã, I. (2020). The Role of Wild Canids in the Seed Dispersal of Washingtonia	Canidae	Seed Dispersal

Citation	Family	Study Focus
Robusta (*Arecaceae*) in Sonoran Desert Oases. *Rev. Mex. Biodivers.* 91. doi:10.22201/IB.20078706E.2020.91.3129.		
Aronne, G., and Russo, D. (1995). Role of Red Fox (*Vulpes vulpes L.*) And Martens (*Martes Spp.*) In Seed Dispersal of *Myrtus communis L.* (*Myrtaceae*). *G. Bot. Ital.* 129, 129. doi:10.1080/11263509509431069.	Canidae, Mustelidae	Seed Dispersal
Aronne, G., and Russo, D. (1997). Carnivorous Mammals as Seed Dispersers of *Myrtus communis* (*Myrtaceae*) In the Mediterranean Shrublands. *Plant Biosyst.* 131, 189–195. doi:10.1080/11263504.1997.10654181.	Canidae, Mustelidae	Seed Dispersal
Ashby, K. R., and Elliot, K. (1983). The Diet of the Badger (*Meles meles L.*) in Castle Eden Dene, County Durham. *Acta Zool. Fenn.* 174, 205–207.	Mustelidae	Frugivory
Auger, J., Meyer, S. E., and Black, H. L. (2002). Are American Black Bears (*Ursus americanus*) Legitimate Seed Dispersers for Fleshy-Fruited Shrubs. *Am. Midl. Nat.* 147, 352–367. doi:10.1674/0003-0031(2002)147[0352:AABBUA]2.0.CO;2.	Ursidae	Seed Dispersal
Baldwin, R. A., and Bender, L. C. (2009). Foods and Nutritional Components of Diets of Black Bear in Rocky Mountain National Park, Colorado. *Can. J. Zool.* 87, 1000–1008. doi:10.1139/Z09-088.	Ursidae	Frugivory
Ball, L. C., and Golightly, R. T. (1992). Energy and Nutrient Assimilation by Gray Foxes on Diets of Mice and Himalaya Berries. *J. Mammal.* 73, 840–846. doi:10.2307/1382205.	Canidae	Frugivory
Barea-Azcón, J. M., Ballesteros-Duperón, E., Gil-Sánchez, J. M., and Virgós, E. (2010). Badger *Meles meles* Feeding Ecology in Dry Mediterranean Environments of the Southwest Edge of Its Distribution Range. *Acta Theriol. (Warsz).* 55, 45–52. doi:10.4098/j.at.0001-7051.048.2008.	Mustelidae	Frugivory
Beck, M. J., and Vander Wall, S. B. (2011). Diplochory in Western Chokecherry: You Can't Judge a Fruit by Its Mesocarp. *Oecologia* 165, 131–141. doi:10.1007/s00442-010-1759-1.	Canidae, Procyonidae, Ursidae	Seed Dispersal
Bello, C., Galetti, M., Montan, D., Pizo, M. A., Mariguela, T. C., Culot, L., et al. (2017). Atlantic Frugivory: A Plant–Frugivore Interaction Data Set for the Atlantic Forest. *Ecology* 98, 1729. doi:10.1002/ecy.1818.	Canidae, Mustelidae, Procyonidae	Frugivory
Bermejo, T., and Guitian, J. (2000). Fruit Consumption by Foxes and Martens in NW Spain in Autumn: A Comparison of Natural and Agricultural Areas. *Folia Zool.* 49, 89–92.	Canidae, Mustelidae	Frugivory
Bermejo, T., Traveset, A., and Willson, M. F. (1998). Post-dispersal Seed Predation in the Temperate Rainforest of Southeast Alaska. *Can. Field-Naturalist* 112, 510–512.	Ursidae	Seed Dispersal

Citation	Family	Study Focus
Bianchi, R. de C., Campos, R. C., Xavier-Filho, N. L., Olifiers, N., Gompper, M. E., and Mourão, G. (2014). Intraspecific, Interspecific, and Seasonal Differences in the Diet of Three Mid-Sized Carnivores in a Large Neotropical Wetland. *Acta Theriol. (Warsz).* 59, 13–23. doi:10.1007/s13364-013-0137-x.	Canidae, Procyonidae	Frugivory
Bisbal, F. J. (1993). Impacto Humano Sobre los Carnivoros de Venezuela. *Stud. Neotrop. Fauna Environ.* 28, 145–156. doi:10.1080/01650529309360899.	Procyonidae	Frugivory
Borchert, M., and Tyler, C. M. (2011). Desiccation Sensitivity and Heat Tolerance of *Prunus ilicifolia* Seeds Dispersed by American Black Bears (*Ursus americanus*). *West. North Am. Nat.* 70, 457–466. doi:10.3398/064.070.0405.	Ursidae	Seed Dispersal
Braid, A. C. R., Manzer, D., and Nielsen, S. E. (2016). Wildlife Habitat Enhancements for Grizzly Bears: Survival Rates of Planted Fruiting Shrubs in Forest Harvests. *For. Ecol. Manage.* 369, 144–154. doi:10.1016/j.foreco.2016.03.032.	Ursidae	Frugivory
Bravo, S. P., Berrondo, M. O., and Cueto, V. R. (2019). Are Small Abandoned Plantations a Threat for Protected Areas in Andean Forests? The Potential Invasion of Non-native Cultivated Species. *Acta Oecologica* 95, 128–134. doi:10.1016/j.actao.2018.11.002.	Canidae	Seed Dispersal
Brunner, H., Harris, R. V., and Amor, R. L. (1976). A note on the Dispersal of Seeds of Blackberry (*Rubus procerus* P.J. Muell.) by Foxes and Emus. *Weed Res.* 16, 171–173. doi:10.1111/j.1365-3180.1976.tb00398.x.	Canidae	Seed Dispersal
Bruun, H. H., Österdahl, S., Moen, J., and Angerbjörn, A. (2005). Distinct Patterns in Alpine Vegetation Around Dens of the Arctic Fox. *Ecography (Cop.).* 28, 81–87. doi:10.1111/j.0906-7590.2005.04033.x.	Canidae	Seed Dispersal
Bustamante, R. O., Simonetti, J. A., and Mella, J. E. (1992). Are Foxes Legitimate and Efficient Seed Dispersers? A Field Test. *Acta Oecologica* 13, 203–208.	Canidae	Seed Dispersal
Campos, C. M., and Ojeda, R. A. (1997). Dispersal and Germination of *Prosopis Flexuosa* (*Fabaceae*) Seeds by Desert Mammals in Argentina. *J. Arid Environ.* 35, 707–714. doi:10.1006/jare.1996.0196.	Canidae	Seed Dispersal
Campos, R. C., Steiner, J., and Zillikens, A. (2012). Bird and Mammal Frugivores of Euterpe Edulis at Santa Catarina Island Monitored by Camera Traps. *Stud. Neotrop. Fauna Environ.* 47, 105–110. doi:10.1080/01650521.2012.678102.	Mustelidae, Procyonidae	Seed Dispersal
Cancio, I., González-Robles, A., Bastida, J. M., Isla, J., Manzaneda, A. J., Salido, T., et al. (2017). Landscape Degradation Affects Red Fox (*Vulpes vulpes*) Diet and Its Ecosystem Services in the Threatened *Ziziphus lotus* Scrubland Habitats of Semiarid Spain. *J. Arid Environ.* 145, 24–34. doi:10.1016/j.jaridenv.2017.05.004.	Canidae	Seed Dispersal

Citation	Family	Study Focus
Cancio, I., González-Robles, A., Bastida, J. M., Manzaneda, A. J., Salido, T., and Rey, P. J. (2016). Habitat Loss Exacerbates Regional Extinction Risk of the Keystone Semiarid Shrub *Ziziphus lotus* Through Collapsing the Seed Dispersal Service by Foxes (*Vulpes vulpes*). *Biodivers. Conserv.* 25, 693–709. doi:10.1007/s10531-016-1085-y.	Canidae	Seed Dispersal
Caryl, F. M., Raynor, R., Quine, C. P., and Park, K. J. (2012). The Seasonal Diet of British Pine Marten Determined From Genetically Identified Scats. *J. Zool.* 288, 252–259. doi:10.1111/j.1469-7998.2012.00951.x.	Mustelidae	Frugivory
Cazetta, E., and Galetti, M. (2009). The Crab-Eating Fox (*Cerdocyon thous*) as a Secondary Seed Disperser of *Eugenia umbelliflora* (*Myrtaceae*) in a Restinga Forest of Southeastern Brazil. *Biota Neotrop.* 9, 271–274. doi:10.1590/S1676-06032009000200027.	Canidae	Seed Dispersal
Celedón-Neghme, C., Traveset, A., and Calviño-Cancela, M. (2013). Contrasting Patterns of Seed Dispersal Between Alien Mammals and Native Lizards in a Declining Plant Species. *Plant Ecol.* 214, 657–667. doi:10.1007/s11258-013-0197-7.	Mustelidae	Seed Dispersal
Chakravarthy, D., and Ratnam, J. (2015). Seed Dispersal of *Vitex glabrata* and *Prunus ceylanica* by Civets (*Viverridae*) in Pakke Tiger Reserve, North-East India: Spatial Patterns and Post-dispersal Seed Fates. *Trop. Conserv. Sci.* 8, 491–504. doi:10.1177/194008291500800213.	Viverridae	Seed Dispersal
Chanthorn, W., Hartig, F., Brockelman, W. Y., Srisang, W., Nathalang, A., and Santon, J. (2019). Defaunation of Large-Bodied Frugivores Reduces Carbon Storage in a Tropical Forest of Southeast Asia. *Sci. Rep.* 9, 1–9. doi:10.1038/s41598-019-46399-y.	Ursidae	Seed Dispersal
Clevenger, A. P. (1996). Frugivory of *Martes martes* and *Genetta genetta* in an Insular Mediterranean Habitat. *Rev. d'Ecologie (La Terre la Vie)* 51, 19–28.	Mustelidae, Viverridae	Frugivory
Coates-Estrada, R., and Estrada, A. (1986). Fruiting and Frugivores at a Strangler Fig in the Tropical Rain Forest of Los Tuxtlas, Mexico. *J. Trop. Ecol.* 2, 349–357. doi:10.1017/S0266467400000985.	Procyonidae	Frugivory
Colon, C. P., and Campos-Arceiz, A. (2013). The Impact of Gut Passage by Binturongs (*Arctictis binturong*) On Seed Germination. *Raffles Bull. Zool.* 61, 417–421.	Viverridae	Seed Dispersal
Colon, C. P., and Sugau, J. B. (2012). Notes on the Diet of the Malay Civet (*Viverra tangalunga*) And Other Civets in Logged and Unlogged Lowland Dipterocarp Rain Forests in Sabah, Borneo. *Malayan Nat. J.* 64, 69–74.	Viverridae	Frugivory

Citation	Family	Study Focus
Corlett, R. T. (1996). Characteristics of Vertebrate-Dispersed Fruits in Hong Kong. *J. Trop. Ecol.* 12, 819–833.	Viverridae	Seed Dispersal
Corlett, R. T. (2011). Seed Dispersal in Hong Kong, China: Past, Present and Possible Futures. *Integr. Zool.* 6, 97–109. doi:10.1111/j.1749-4877.2011.00235.x.	Viverridae	Seed Dispersal
Corlett, R. T. (2017). Frugivory and Seed Dispersal by Vertebrates in Tropical and Subtropical Asia: An Update. *Glob. Ecol. Conserv.* 11, 1–22. doi:10.1016/j.gecco.2017.04.007.	Canidae, Hyaenidae, Mustelidae, Ursidae, Viverridae	Frugivory
Cypher, B. L., and Cypher, E. A. (1999). Germination Rates of Tree Seeds Ingested by Coyotes and Raccoons. *Am. Midl. Nat.* 142, 71–76. doi:10.1674/0003-0031(1999)142[0071:GROTSI]2.0.CO;2.	Canidae, Procyonidae	Seed Dispersal
Czernik, M., Kowalczyk, R., and Zalewski, A. (2016). Spatio-Temporal Variation of Predator Diet in a Rural Habitat: Stone Martens in the Villages of BiałOwieża Forest. *Mammal Res.* 61, 187–196. doi:10.1007/s13364-016-0273-1.	Mustelidae	Frugivory
D'hondt, B., Vansteenbrugge, L., van den Berge, K., Bastiaens, J., and Hoffmann, M. (2011). Scat Analysis Reveals a Wide Set of Plant Species to Be Potentially Dispersed by Foxes. *Plant Ecol. Evol.* 144, 106–110. doi:10.5091/plecevo.2011.472.	Canidae	Seed Dispersal
Dahlin, K. M., Asner, G. P., and Field, C. B. (2014). Linking Vegetation Patterns to Environmental Gradients and Human Impacts in a Mediterranean-Type Island Ecosystem. *Landsc. Ecol.* 29, 1571–1585. doi:10.1007/s10980-014-0076-1.	Canidae	Seed Dispersal
Deacon, D. C., Happe, C. L., Chen, C., Tedeschi, N., Manso, A. M., Li, T., et al. (2014). Dietary Analysis of Raccoons Captured in Yokohama, Eastern Japan. *Japanese J. Conserv. Ecol.* 19, 87–93.	Procyonidae	Frugivory
Dellafiore, C. M. (2018). Does the Pampas fox (*Lycalopex gymnocercus*) Affect Firethorn (*Pyracantha atalantoides*) Germination? *Mastozoología Neotrop.* 25, 053–058. doi:10.31687/saremmn.18.25.1.0.06.	Canidae	Seed Dispersal
Díaz-Ruiz, F., Delibes-Mateos, M., García-Moreno, J. L., María López-Martín, J., Ferreira, C., and Ferreras, P. (2013). Biogeographical Patterns in the Diet of an Opportunistic Predator: The Red Fox *Vulpes vulpes* in the Iberian Peninsula. *Mamm. Rev.* 43, 59–70. doi:10.1111/j.1365-2907.2011.00206.x.	Canidae	Frugivory
Dumond, M., Villard, M. A., and Tremblay, É. (2001). Does Coyote Diet Vary Seasonally Between a Protected and an Unprotected Forest Landscape? *Ecoscience* 8, 301–310. doi:10.1080/11956860.2001.11682657.	Canidae	Frugivory
Elgmork, K. K. K., and Kaasa, J. (1992). Food Habits and Foraging of the Brown Bear *Ursus arctos* in Central South Norway.	Ursidae	Frugivory

Citation	Family	Study Focus
Ecography, Copenhagen 15, 101–110. doi:10.1111/j.1600-0587.1992.tb00013.x.		
Enders, M. S., and Vander Wall, S. B. (2012). Black Bears Ursus americanus Are Effective Seed Dispersers, With a Little Help From Their Friends. *Oikos* 121, 589–596. doi:10.1111/j.1600-0706.2011.19710.x.	Ursidae	Seed Dispersal
Enomoto, T., Saito, M. U., Yoshikawa, M., and Kaneko, Y. (2018). Winter Diet of the Raccoon Dog (Nyctereutes procyonoides) in Urban Parks, Central Tokyo. *Mammal Study* 43, 275–280. doi:10.3106/ms2018-0024.	Canidae	Frugivory
Escribano-Avila, G. (2019). Non-specialized Frugivores as Key Seed Dispersers in Dry Disturbed Environments: An Example With a Generalist Neotropical Mesocarnivore. *J. Arid Environ.* 167, 18–25. doi:10.1016/j.jaridenv.2019.04.015.	Canidae	Seed Dispersal
Escribano-Avila, G., Calviño-Cancela, M., Pías, B., Virgós, E., Valladares, F., and Escudero, A. (2014). Diverse Guilds Provide Complementary Dispersal Services in a Woodland Expansion Process After Land Abandonment. *J. Appl. Ecol.* 51, 1701–1711. doi:10.1111/1365-2664.12340.	Canidae, Mustelidae	Seed Dispersal
Escribano-Ávila, G., Pías, B., Sanz-Pérez, V., Virgós, E., Escudero, A., and Valladares, F. (2013). Spanish Juniper Gain Expansion Opportunities by Counting on a Functionally Diverse Dispersal Assemblage Community. *Ecol. Evol.* 3, 3751–3763. doi:10.1002/ece3.753.	Canidae, Mustelidae	Seed Dispersal
Escribano-Avila, G., Sanz-Pérez, V., Pías, B., Virgós, E., Escudero, A., and Valladares, F. (2012). Colonization of Abandoned Land by *Juniperus thurifera* Is Mediated by the Interaction of a Diverse Dispersal Assemblage and Environmental Heterogeneity. *PLoS One* 7, 1–10. doi:10.1371/journal.pone.0046993.	Canidae, Mustelidae	Seed Dispersal
Fahimi, H., Qashqaei, A. T., Chalani, M., Asadi, Z., Broomand, S., Ahmadi, N., et al. (2018). Evidence of Seed Germination in Scats of the Asiatic Black Bear *Ursus thibetanus* in Iran (*Mammalia: Carnivora*). *Zool. Middle East* 64, 182–184. doi:10.1080/09397140.2018.1444573.	Ursidae	Seed Dispersal
Farris, E., Canopoli, L., Cucca, E., Landi, S., Maccioni, A., and Filigheddu, R. (2017). Foxes Provide a Direct Dispersal Service to Phoenician Junipers in Mediterranean Coastal Environments: Ecological and Evolutionary Implications. *Plant Ecol. Evol.* 150, 117–128. doi:10.5091/plecevo.2017.1277.	Canidae	Seed Dispersal
Fedriani, J. M., and Delibes, M. (2009). Functional Diversity in Fruit-Frugivore Interactions: A Field Experiment With Mediterranean Mammals. Ecography (Cop.). 32, 983–992. doi:10.1111/j.1600-0587.2009.05925.x.	Canidae, Mustelidae	Frugivory

Citation	Family	Study Focus
Fedriani, J. M., and Delibes, M. (2009). Seed Dispersal in the Iberian Pear, Pyrus bourgaeana: A Role for Infrequent Mutualists. Ecoscience 16, 311–321. doi:10.2980/16-3-3253.	Canidae, Mustelidae	Seed Dispersal
Fedriani, J. M., and Delibes, M. (2011). Dangerous liaisons disperse the mediterranean dwarf palm:Fleshy-Pulp defensive role against seed predators. *Ecology* 92, 304–315. doi:10.1890/09-2194.1.	Mustelidae	Frugivory
Fedriani, J. M., and Delibes, M. (2013). Pulp Feeders Alter Plant Interactions With Subsequent Animal Associates. *J. Ecol.* 101, 1581–1588. doi:10.1111/1365-2745.12146.	Canidae, Mustelidae	Seed Dispersal
Fedriani, J. M., Wiegand, T., Ayllón, D., Palomares, F., Suárez-Esteban, A., and Grimm, V. (2018). Assisting Seed Dispersers to Restore Oldfields: An Individual-Based Model of the Interactions Among Badgers, Foxes and Iberian Pear Trees. *J. Appl. Ecol.* 55, 600–611. doi:10.1111/1365-2664.13000.	Canidae, Mustelidae	Seed Dispersal
Fedriani, J. M., Wiegand, T., and Delibes, M. (2010). Spatial Pattern of Adult Trees and the Mammal-Generated Seed Rain in the Iberian Pear. *Ecography (Cop.).* 33, 545–555. doi:10.1111/j.1600-0587.2009.06052.x.	Canidae, Mustelidae	Seed Dispersal
Fernández, C., and Puerta-Piñero, C. (2019). Mammal Diversity and Its Relationship With Endozoochorous Seed Dispersal in Vineyards. *Ecosistemas* 28, 126–141.	Canidae, Mustelidae	Seed Dispersal
Fortin, J. K., Farley, S. D., Rode, K. D., and Robbins, C. T. (2007). Dietary and Spatial Overlap Between Sympatric Ursids Relative to Salmon Use. *Ursus* 18, 19–29. doi:10.2192/1537-6176(2007)18[19:DASOBS]2.0.CO;2.	Ursidae	Frugivory
Francisco, J., and Bisbal, E. (1986). Food Habits of Some Neotropical Carnivores in Venezuela (*Mammalia, Carnivora*). *Mammalia* 50, 329–340. doi:10.1515/mamm.1986.50.3.329.	Mustelidae, Procyonidae	Frugivory
Fredriksson, G. M., Wich, S. A., and Trisno (2006). Frugivory in Sun Bears (*Helarctos malayanus*) Is Linked to El NIño-Related Fluctuations in Fruiting Phenology, East Kalimantan, Indonesia. *Biol. J. Linn. Soc.* 89, 489–508. doi:10.1111/j.1095-8312.2006.00688.x.	Ursidae	Frugivory
Furubayashi, K. (2008). Fruit Phenology of *Prunus jamasakura* and the Feeding Habit of the Asiatic Black Bear as a Seed Disperser. 385–392. doi:10.1007/s11284-007-0399-3.	Ursidae	Seed Dispersal
Gable, T. D., Windels, S. K., and Bruggink, J. G. (2017). Estimating Biomass of Berries Consumed by Gray Wolves. *Wildl. Soc. Bull.* 41, 129–131. doi:10.1002/wsb.730.	Canidae	Frugivory
Garbary, D. J., Hill, N. M., and Miller, A. G. (2013). Invasion of *Rosa rugosa* (Rugosa Rose) Into Coastal Plant Communities of	Canidae, Mustelidae	Seed Dispersal

Citation	Family	Study Focus
Brier Island, Nova Scotia. *Can. Field-Naturalist* 127, 319–331. doi:10.22621/cfn.v127i4.1513.		
García-Robledo, C., and Kuprewicz, E. K. (2009). Vertebrate Fruit Removal and Ant Seed Dispersal in the Neotropical Ginger *Renealmia alpinia* (*Zingiberaceae*). *Biotropica* 41, 209–214. doi:10.1111/j.1744-7429.2008.00478.x.	Procyonidae	Seed Dispersal
Gazzola, A., and Balestrieri, A. (2020). Nutritional Ecology Provides Insights Into Competitive Interactions Between Closely Related Martes Species. *Mamm. Rev.* 50, 82–90. doi:10.1111/mam.12177.	Mustelidae	Frugivory
Geffen, E., Hefner, R., Macdonald, D. W., and Ucko, M. (1992). Diet and Foraging Behavior of Blanford's Foxes, *Vulpes cana*, in Israel. *Am. Soc. Mammal.* 73, 395–402.	Canidae	Frugivory
Goldenberg, M., Goldenberg, F., Funk, S. M., Henschel, J., and Millesi, E. (2010). Diet Composition of Black-Backed Jackals, *Canis mesomelas* in the Namib Desert. *Folia Zool.* 59, 93–101. doi:10.25225/fozo.v59.i2.a3.2010.	Canidae	Frugivory
González-Varo, J. P., López-Bao, J. V., and Guitián, J. (2013). Functional Diversity Among Seed Dispersal Kernels Generated by Carnivorous Mammals. *J. Anim. Ecol.* 82, 562–571. doi:10.1111/1365-2656.12024.	Canidae, Mustelidae	Seed Dispersal
González-Varo, J. P., López-Bao, J. V., and Guitián, J. (2017). Seed Dispersers Help Plants to Escape Global Warming. *Oikos* 126, 1600–1606. doi:10.1111/oik.04508.	Canidae, Mustelidae	Seed Dispersal
Gormezano, L. J., and Rockwell, R. F. (2013). Dietary Composition and Spatial Patterns of Polar Bear Foraging on Land in Western Hudson Bay. *BMC Ecol.* 13, 13.	Ursidae	Frugivory
Graae, B. J., Pagh, S., Bruun, H. H., and Bruunà, H. H. (2004). An Experimental Evaluation of the Arctic Fox (*Alopex lagopus*) as a Seed Disperser. *Arctic, Antarct. Alp. Res.* 36, 468–473. doi:10.1657/1523-0430(2004)036.	Canidae	Seed Dispersal
Grünewald, C., Breitbach, N., and Böhning-Gaese, K. (2010). Tree Visitation and Seed Dispersal of Wild Cherries by Terrestrial Mammals Along a Human Land-Use Gradient. *Basic Appl. Ecol.* 11, 532–541. doi:10.1016/j.baae.2010.07.007.	Canidae, Mustelidae	Seed Dispersal
Guharajan, R., Arnold, T. W., Bolongon, G., Dibden, G. H., Abram, N. K., Teoh, S. W., et al. (2018). Survival Strategies of a Frugivore, the Sun Bear, in a Forest-Oil Palm Landscape. *Biodivers. Conserv.* 27, 3657–3677. doi:10.1007/s10531-018-1619-6.	Ursidae	Frugivory
Guitián, J., and Munilla, I. (2010). Responses of Mammal Dispersers to Fruit Availability: Rowan (*Sorbus aucuparia*) and Carnivores in Mountain Habitats of Northern Spain. *Acta Oecologica* 36, 242–247. doi:10.1016/j.actao.2010.01.005.	Canidae, Mustelidae	Seed Dispersal

Citation	Family	Study Focus
Haba, C., Oshida, T., Sasaki, M., Endo, H., Ichikawa, H., and Masuda, Y. (2008). Morphological Variation of the Japanese Raccoon Dog: Implications for Geographical Isolation and Environmental Adaptation. *J. Zool.* 274, 239–247. doi:10.1111/j.1469-7998.2007.00376.x.	Canidae	Frugivory
Hall, D. L., and Frcpc, F. (2002). Endozoochorous Seed Dispersal by Martens (*Martes foina, M. martes*) in Two Woodland Habitats. *Flora* 197, 370–378.	Mustelidae	Seed Dispersal
Harrer, L. E. F., and Levi, T. (2018). The Primacy of Bears as Seed Dispersers in Salmon-Bearing Ecosystems. *Ecosphere* 9. doi:10.1002/ecs2.2076.	Ursidae	Seed Dispersal
Helbig-bonitz, M., Rutten, G., and Kalko, K. V (2013). Tree Seed Dispersal by African Civets in the Afromontane Highlands: Too Long a Latrine to Be Effective for Tree Population Dynamics. *Afr. J. Ecol.* 52, 122–125. doi:10.1111/aje.12090.	Viverridae	Seed Dispersal
Hernandez, A. (1993). The Role of Birds and Mammals in the Dispersal Ecology of *Rhamnus alpinus* (*Rhamnaceae*) In the Cantabrian Mts. *Folia Zool.* 42, 105–109.	Canidae, Mustelidae	Seed Dispersal
Hernández, Á. (2008). Cherry Removal by Seed-Dispersing Mammals: Mutualism Through Commensal Association With Frugivorous Birds. *Polish J. Ecol.* 56, 127–138.	Canidae, Mustelidae	Seed Dispersal
Hernández, Á., and Zaldívar, P. (2016). Ecology of Stoats *Mustela erminea* in a Valley of the Cantabrian Mountains, Northwestern Spain. *Vertebr. Zool.* 66, 225–238.	Mustelidae	Frugivory
Herrera, C. M. (1989). Frugivory and Seed Dispersal by Carnivorous Mammals, and Associated Fruit Characteristics, in Undisturbed Mediterranean Habitats. *Oikos* 55, 250–262.	Canidae, Mustelidae	Seed Dispersal
Herrera, J. M., de Sá Teixeira, I., Rodríguez-Pérez, J., and Mira, A. (2016). Landscape Structure Shapes Carnivore-Mediated Seed Dispersal Kernels. *Landsc. Ecol.* 31, 731–743. doi:10.1007/s10980-015-0283-4.	Canidae, Herpestidae, Mustelidae, Viverridae	Seed Dispersal
Hewitt, N., and Miyanishi, K. (1997). The Role of Mammals in Maintaining Plant Species Richness in a Floating Typha Marsh in Southern Ontario. *Biodivers. Conserv.* 6, 1085–1102. doi:10.1023/A:1018380000881.	Procyonidae	Seed Dispersal
Heydon, M. J., and Bulloh, P. (1996). The Impact of Selective Logging on Sympatric Civet Species in Borneo. *Oryx* 30, 31–36. doi:10.1017/s0030605300021360.	Canidae, Viverridae	Frugivory
Hickey, J. R., Flynn, R. W., Buskirk, S. W., Gerow, K. G., and Willson, M. F. (1999). An Evaluation of a Mammalian Predator, *Martes americana*, as a Disperser of Seeds. *Oikos* 87, 499. doi:10.2307/3546814.	Mustelidae	Seed Dispersal

Citation	Family	Study Focus
Hill, N. M., van der Kloet, S. P., and Garbary, D. J. (2012). The Regeneration Ecology of *Empetrum nigrum*, the Black Crowberry, on Coastal Heathland in Nova Scotia. *Botany* 90, 379–392. doi:10.1139/B2012-022.	Mustelidae	Seed Dispersal
Hirsch, B. (2009). Seasonal variation in the diet of ring-tailed coatis (Nasua nasua) in iguazu, Argentina. *J. Mammal.* 90, 136–143. doi:10.1644/08-MAMM-A-050.1.	Procyonidae	Frugivory
Hisano, M., and Deguchi, S. (2018). Reviewing Frugivory Characteristics of the Japanese Marten (*Martes melampus*). *Zool. Ecol.* 28, 10–20. doi:10.1080/21658005.2017.1412017.	Mustelidae	Frugivory
Hobson, K. A., Stirling, I., and Andriashek, D. S. (2009). Isotopic Homogeneity of Breath CO2 From Fasting and Berry-Eating Polar Bears: Implications for Tracing Reliance on Terrestrial Foods in a Changing Arctic. *Can. J. Zool.* 87, 50–55. doi:10.1139/Z08-137.	Ursidae	Frugivory
Holisova, V., and Obrtel, R. (1982). Scat Analytical Data on the Diet of Urban Stone Martens, *Martes foina* (*Mustelidae, Mammalia*). *Folia Zool. (Zoologicke List.* 31, 21–30.	Mustelidae	Frugivory
Horvitz, C. C., Koop, A. L., and Erickson, K. D. (2015). Time-Invariant and Stochastic Disperser-Structured Matrix Models: Invasion Rates of Fleshy-Fruited Exotic Shrubs. *Discret. Contin. Dyn. Syst. - Ser. B* 20, 1639–1662. doi:10.3934/dcdsb.2015.20.1639.	Procyonidae	Seed Dispersal
Iwama, M., Yamazaki, K., Matsuyama, M., Hoshino, Y., Hisano, M., Newman, C., et al. (2017). Masked Palm Civet *Paguma larvata* Summer Diet Differs between Sexes in a Suburban Area of Central Japan. *Mammal Study* 42, 185–190. doi:10.3106/041.042.0301.	Viverridae	Frugivory
Jiménez, J. E. (2007). Ecology of a Coastal Population of the Critically Endangered Darwin's Fox (*Pseudalopex fulvipes*) On Chiloé Island, Southern Chile. *J. Zool.* 271, 63–77. doi:10.1111/j.1469-7998.2006.00218.x.	Canidae	Frugivory
Jordano, P., Garcia, C., Godoy, J. A., Garcia-Castano, J. L., and García-Castaño, J. L. (2007). Differential Contribution of Frugivores to Complex Seed Dispersal Patterns. *Proc. Natl. Acad. Sci. U. S. A.* 104, 3278–3282. doi:10.1073/pnas.0606793104.	Canidae, Mustelidae	Frugivory
Juan, T., Sagrario, A., Jesús, H., and Cristina, C. M. (2006). Red Fox (*Vulpes vulpes L.*) Favour Seed Dispersal, Germination and Seedling Survival of Mediterranean Hackberry (*Celtis australis L.*). *Acta Oecologica* 30, 39–45. doi:10.1016/j.actao.2006.01.004.	Canidae	Seed Dispersal
Julien-Laferriere, D. (1993). Radio-Tracking Observations on Ranging and Foraging Patterns by Kinkajous (*Potos flavus*) in French Guiana. *J. Trop. Ecol.* 9, 19–32. doi:10.1017/S0266467400006908.	Procyonidae	Frugivory

Citation	Family	Study Focus
Julien-Laferrière, D. (1999). Foraging Strategies and Food Partitioning in the Neotropical Frugivorous Mammals *Caluromys philander* and *Potos flavus*. *J. Zool.* 247, 71–80. doi:10.1017/S0952836999001077.	Procyonidae	Frugivory
Kamler, J. F., Klare, U., and Macdonald, D. W. (2020). Seed Dispersal Potential of Jackals and Foxes in Semi-arid Habitats of South Africa. *J. Arid Environ.* 183, 104284. doi:10.1016/j.jaridenv.2020.104284.	Canidae	Seed Dispersal
Karimi, S., Hemami, M. R., Tarkesh Esfahani, M., Akhani, H., and Baltzinger, C. (2018). Complementary Endozoochorous Seed Dispersal by Large Mammals in the Golestan National Park, Iran. *Seed Sci. Res.* 28, 294–302. doi:10.1017/S0960258518000351.	Ursidae	Seed Dispersal
Karimi, S., Hemami, M. R., Tarkesh Esfahani, M., and Baltzinger, C. (2020). Endozoochorous Dispersal by Herbivores and Omnivores Is Mediated by Germination Conditions. *BMC Ecol.* 20, 1–14. doi:10.1186/s12898-020-00317-3.	Ursidae	Seed Dispersal
Kays, R. W. (1999). Food preferences of Kinkajous (<i>Potos flavus</>): A Frugivorous Carnivore. *J. Mammal.* 80, 589–599. doi:10.2307/1383303.	Procyonidae	Frugivory
Kitamura, S., and Poonswad, P. (2013). Nutmeg-Vertebrate Interactions in the Asia-Pacific Region: Importance of Frugivores for Seed Dispersal in *Myristicaceae*. *Trop. Conserv. Sci.* 6, 608–636. doi:10.1177/194008291300600503.	Ursidae, Viverridae	Seed Dispersal
Kitamura, S., Yumoto, T., Poonswad, P., Chuailua, P., Plongmai, K., Maruhashi, T., et al. (2002). Interactions Between Fleshy Fruits and Frugivores in a Tropical Seasonal Forest in Thailand. *Oecologia* 133, 559–572. doi:10.1007/s00442-002-1073-7.	Ursidae, Viverridae	Frugivory
Koike, S., and Masaki, T. (2008). Frugivory of Carnivora in Central and Southern Parts of Japan Analyzed by Literature Search. *J. Japanese For. Soc.* 90, 26–35. Available at: http://www.google.com/patents?hl=en&lr=&vid=USPAT3101219&id=hxZKAAAAEBAJ&oi=fnd&dq=Herrera&printsec=abstract%5Cnhttp://joi.jlc.jst.go.jp/JST.JSTAGE/jfs/90.26?from=Google.	Canidae, Mustelidae, Ursidae	Frugivory
Koike, S., and Masaki, T. (2019). Characteristics of Fruits Consumed by Mammalian Frugivores in Japanese Temperate Forest. *Ecol. Res.* 34, 246–254. doi:10.1111/1440-1703.1057.	Canidae, Mustelidae, Ursidae	Frugivory
Koike, S., Masaki, T., Nemoto, Y., Kozakai, C., Yamazaki, K., Kasai, S., et al. (2011). Estimate of the Seed Shadow Created by the Asiatic Black Bear Ursus thibetanus and Its Characteristics as a Seed Disperser in Japanese Cool-Temperate Forest. *Oikos* 120, 280–290. doi:10.1111/j.1600-0706.2010.18626.x.	Ursidae	Seed Dispersal

Citation	Family	Study Focus
Koike, S., Morimoto, H., Goto, Y., Kozakai, C., and Yamazaki, K. (2008). Frugivory of Carnivores and Seed Dispersal of Fleshy Fruits in Cool-Temperate Deciduous Forests. *J. For. Res.* 13, 215–222. doi:10.1007/s10310-008-0069-5.	Canidae, Mustelidae, Ursidae	Seed Dispersal
Koike, S., Morimoto, H., Kozakai, C., Arimoto, I., Yamazaki, K., Iwaoka, M., et al. (2012). Seed Removal and Survival in Asiatic Black Bear *Ursus thibetanus* Faeces: Effect of Rodents as Secondary Seed Dispersers. *Wildlife Biol.* 18, 24–34. doi:10.2981/10-049.	Ursidae	Seed Dispersal
Kulavmode, A. R., Hegde, V. M., and Kambale, A. A. (2015). A Note on Seed Dispersal of Rock Banana *Ensete superbum* by Aslan Palm Civet *Paradoxurus hermaphrodltus* at Sinhgad Fort, Maharashtra, India. *J. Bombay Nat. Hist. Soc.* 112, 25–52.	Viverridae	Seed Dispersal
Kurek, P. (2015). Consumption of Fleshy Fruit: Are Central European Carnivores Really Less Frugivorous Than Southern European Carnivores? *Mamm. Biol.* 80, 365–372. doi:10.1016/j.mambio.2015.05.006.	Canidae, Mustelidae	Frugivory
Kurek, P., and Holeksa, J. (2015). Toxic Fruits in the Diet of Carnivores in Poland. *Ann. Zool. Fennici* 52, 186–192. doi:10.5735/086.052.0306.	Canidae, Mustelidae	Frugivory
Kurek, P., Kapusta, P., and Holeksa, J. (2014). Burrowing by Badgers (*Meles meles*) and Foxes (*Vulpes vulpes*) Changes Soil Conditions and Vegetation in a European Temperate Forest. *Ecol. Res.* 29, 1–11. doi:10.1007/s11284-013-1094-1.	Canidae, Mustelidae	Seed Dispersal
Lalleroni, A., Quenette, P. Y., Daufresne, T., Pellerin, M., and Baltzinger, C. (2017). Exploring the Potential of Brown Bear (*Ursus arctos arctos*) As a Long-Distance Seed Disperser: A Pilot Study in South-Western Europe. *Mammalia* 81, 1–9. doi:10.1515/mammalia-2015-0092.	Ursidae	Seed Dispersal
Lambert, J. E., Fellner, V., McKenney, E., and Hartstone-Rose, A. (2014). Binturong (*Arctictis binturong*) And Kinkajou (*Potos flavus*) Digestive Strategy: Implications for Interpreting Frugivory in Carnivora and Primates. *PLoS One* 9. doi:10.1371/journal.pone.0105415.	Procyonidae, Viverridae	Frugivory
Lanszki, Z., Purger, J. J., Bocz, R., Szép, D., and Lanszki, J. (2019). The Stone Marten and the Red Fox Consumed Predominantly Fruits All Year Round: A Case Study. *Acta Zool. Acad. Sci. Hungaricae* 65, 45–62. doi:10.17109/AZH.65.1.45.2019.	Canidae, Mustelidae	Frugivory
Larson, R. N., Brown, J. L., Karels, T., and Riley, S. P. D. (2020). Effects of Urbanization on Resource Use and Individual Specialization in Coyotes (*Canis latrans*) in Southern California. *PLoS One* 15, 1–23. doi:10.1371/journal.pone.0228881.	Canidae	Frugivory

Citation	Family	Study Focus
Larson, R. N., Morin, D. J., Wierzbowska, I. A., and Crooks, K. R. (2015). Food Habits of Coyotes, Gray Foxes, and Bobcats in a Coastal Southern California Urban Landscape. *West. North Am. Nat.* 75, 339–347. doi:10.3398/064.075.0311.	Canidae	Frugivory
Lautenschlager, R. A. (1997). Effects of Perturbations and Stimulants on Red Raspberry (*Rubus idaeus L.*) Seed Germination. *For. Chron.* 73, 453–457. doi:10.5558/tfc73453-4.	Canidae, Ursidae	Seed Dispersal
Lázaro-Nogal, A., Matesanz, S., García-Fernández, A., Traveset, A., and Valladares, F. (2017). Population Size, Center–Periphery, and Seed Dispersers' Effects on the Genetic Diversity and Population Structure of the Mediterranean Relict Shrub *Cneorum tricoccon*. *Ecol. Evol.* 7, 7231–7242. doi:10.1002/ece3.2940.	Mustelidae	Seed Dispersal
Leakey, L. N., Milledge, S. A. H., Leakey, S. M., Edung, J., Haynes, P., Kiptoo, D. K., et al. (1999). Diet of Striped Hyaena in Northern Kenya. *Afr. J. Ecol.* 37, 314–326. doi:10.1046/j.1365-2028.1999.00180.x.	Hyaenidae	Frugivory
de Lima, R. E. M., de Sá Dechoum, M., and Castellani, T. T. (2015). Native Seed Dispersers May Promote the Spread of the Invasive Japanese Raisin Tree (*Hovenia dulcis* Thunb.) In Seasonal Deciduous Forest in Southern Brazil. *Trop. Conserv. Sci.* 8, 846–862. doi:10.1177/194008291500800318.	Canidae	Seed Dispersal
Logiudice, K. (2001). Latrine Foraging Strategies of Two Small Mammals: Implications for the Transmission of *Baylisascaris procyonis*. *Am. Midl. Nat.* 146, 369–378. doi:10.1674/0003-0031(2001)146[0369:LFSOTS]2.0.CO;2.	Procyonidae	Frugivory
LoGiudice, K., and Ostfeld, R. (2002). Interactions Between Mammals and Trees: Predation on Mammal-Dispersed Seeds and the Effect of Ambient Food. *Oecologia* 130, 420–425. doi:10.1007/s004420100810.	Procyonidae	Seed Dispersal
López-Bao, J. V., and González-Varo, J. P. (2011). Frugivory and Spatial Patterns of Seed Deposition by Carnivorous Mammals in Anthropogenic Landscapes: A Multi-Scale Approach. *PLoS One* 6, 19–21. doi:10.1371/journal.pone.0014569.	Canidae, Mustelidae	Seed Dispersal
López-Bao, J. V., González-Varo, J. P., and Guitián, J. (2015). Mutualistic Relationships Under Landscape Change: Carnivorous Mammals and Plants After 30 Years of Land Abandonment. *Basic Appl. Ecol.* 16, 152–161. doi:10.1016/j.baae.2014.12.001.	Canidae, Mustelidae	Seed Dispersal
Maldonado, D. E., Loayza, A. P., Garcia, E., and Pacheco, L. F. (2018). Qualitative Aspects of the Effectiveness of Culpeo Foxes (Lycalopex culpaeus) as Dispersers of Prosopis alba (Fabaceae) in a Bolivian Dry Valley. *Acta Oecologica* 87, 29–33. doi:10.1016/j.actao.2018.02.005.	Canidae	Seed Dispersal

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Mandujano, M. D. C., Golubov, J., and Montaña, C. (1997). Dormancy and Endozoochorous Dispersal of *Opuntia rastrera* Seeds in the Southern Chihuahuan Desert. *J. Arid Environ.* 36, 259–266. doi:10.1006/jare.1996.0210.	Canidae	Seed Dispersal
Marod, D., Pinyo, P., Duengkae, P., and Hiroshi, T. (2010). The Role of Wild Banana (*Musa acuminata* Colla) On Wildlife Diversity in Mixed Deciduous Forest, Kanchanaburi Province, Western Thailand. *Kasetsart J. - Nat. Sci.* 44, 35–43.	Viverridae	Seed Dispersal
Márquez, G., and Pacheco, V. (2011). Nuevas Evidencias de la Presencia Del Oso Andino (*Tremarctos ornatus*) En Las Yungas de Puno, El Registro Más Austral de Perú. *Rev. Peru. Biol.* 17, 377–380. doi:10.15381/rpb.v17i3.14.	Ursidae	Frugivory
Martínez, I., García, D., and Obeso, J. R. (2008). Differential Seed Dispersal Patterns Generated by a Common Assemblage of Vertebrate Frugivores in Three Fleshy-Fruited Trees. *Ecoscience* 15, 189–199. doi:10.2980/15-2-3096.	Canidae, Mustelidae	Seed Dispersal
Martinoli, A., Preatoni, D. G., Chiarenzi, B., Wauters, L. A., and Tosi, G. (2001). Diet of Stoats (*Mustela erminea*) in an Alpine Habitat: The Importance of Fruit Consumption in Summer. *Acta Oecologica* 22, 45–53. doi:10.1016/S1146-609X(01)01102-X.	Mustelidae	Frugivory
Masaki, T. (2009). Current and Future Studies on Seed Dispersal by Vertebrates in Japan. *Japanese J. Ecol.* 59, 13–24. doi:10.18960/seitai.59.1_13.	Ursidae	Seed Dispersal
Masaki, T., Takahashi, K., Sawa, A., Kado, T., Naoe, S., Koike, S., et al. (2012). Fleshy Fruit Characteristics in a Temperate Deciduous Forest of Japan: How Unique Are They? *J. Plant Res.* 125, 103–114. doi:10.1007/s10265-011-0423-0.	Ursidae	Frugivory
Matías, L., Zamora, R., Mendoza, I., and Hódar, J. A. (2010). Seed Dispersal Patterns by Large Frugivorous Mammals in a Degraded Mosaic Landscape. *Restor. Ecol.* 18, 619–627. doi:10.1111/j.1526-100X.2008.00475.x.	Canidae, Mustelidae	Seed Dispersal
Matsuo, R., and Ochiai, K. (2009). Dietary Overlap Among Two Introduced and One Native Sympatric Carnivore Species, the Raccoon, the Masked Palm Civet, and the Raccoon Dog, in Chiba Prefecture, Japan. *Mammal Study* 34, 187–194. doi:10.3106/041.034.0402.	Canidae, Procyonidae, Viverridae	Frugivory
Mattson, D. J., Blanchard, B. M., and Knight, R. R. (1991). Food Habits of Yellowstone Grizzly Bears, 1977-1987. *Can. J. Zool.* 69, 1619–1629. doi:10.1139/z91-226.	Ursidae	Frugivory
McConkey, K., and Galetti, M. (1999). Seed Dispersal by the Sun Bear *Helarctos malayanus* in Central Borneo. *J. Trop. Ecol.* 15, 237–241.	Ursidae	Seed Dispersal
McConkey, K. R., Nathalang, A., Brockelman, W. Y., Saralamba, C., Santon, J., Matmoon, U., et al. (2018). Different Megafauna	Ursidae	Seed Dispersal

Citation	Family	Study Focus
Vary in Their Seed Dispersal Effectiveness of the Megafaunal Fruit *Platymitra macrocarpa* (*Annonaceae*). *PLoS One* 13, 1–18. doi:10.1371/journal.pone.0198960.		
McKinney, T., and Smith, T. W. (2007). Diets of Sympatric Bobcats and Coyotes During Years of Varying Rainfall in Central Arizona. *West. North Am. Nat.* 67, 8–15. doi:10.3398/1527-0904(2007)67[8:DOSBAC]2.0.CO;2.	Canidae	Frugivory
Mendoza, E., Camargo-Sanabria, A. A., Basurto-Godoy, J., Godínez-Gómez, O., and Mendoza, M. (2019). Activity Patterns of Terrestrial Frugivorous Mammals in a Mexican Neotropical Forest. *Therya* 10, 371–380. doi:10.12933/therya-19-876.	Procyonidae	Frugivory
Milton, S. J., and Dean, W. R. J. (2001). Seeds Dispersed in Dung of Insectivores and Herbivores in Semi-arid Southern Africa. *J. Arid Environ.* 47, 465–483. doi:10.1006/jare.2000.0727.	Canidae	Seed Dispersal
Mise, Y., Yamazaki, K., Soga, M., and Koike, S. (2016). Comparing Methods of Acquiring Mammalian Endozoochorous Seed Dispersal Distance Distributions. *Ecol. Res.* 31, 881–889. doi:10.1007/s11284-016-1397-0.	Canidae	Seed Dispersal
Mitani, M., Yokoyama, M., and Kishimoto, M. (2002). Spatial Distribution and Foraging Habits of Mammals in the Rokkou Mountains on the Basis of Trace Detection and Fecal Analyses in Fruiting Seasons in September and October. *Humans Nat.* 13, 57–66. doi:10.24713/hitotoshizen.13.0_57.	Canidae, Mustelidae	Frugivory
Morales-Paredes, C., Valdivia, C. E., and Sade, S. (2015). Frugivory by Native (*Lycalopex* Spp.) And Allochthonous (*Canis lupus familiaris*) Canids Reduces the Seed Germination of Litre (*Lithrea caustica*) In Central Chile. *Bosque* 36, 481–486. doi:10.4067/S0717-92002015000300014.	Canidae	Seed Dispersal
Mori, T., Nakata, S., and Izumiyama, S. (2019). Dietary Specialization Depending on Ecological Context and Sexual Differences in Asiatic Black Bears. *PLoS One* 14, 1–15. doi:10.1371/journal.pone.0223911.	Ursidae	Frugivory
Motta-Junior, J. C., Lombardi, J. A., and Talamoni, S. A. (1994). Notes on Crab-Eating Fox (*Dusicyon thous*) Seed Dispersal and Food Habits in Southeastern Brazil. *Mammalia* 58, 156–159.	Canidae	Seed Dispersal
Mudappa, D., Kumar, A., and Chellam, R. (2010). Diet and Fruit Choice of the Brown Palm Civet *Paradoxurus jerdoni*, a Viverrid Endemic to the Western Ghats Rainforest, India. *Trop. Conserv. Sci.* 3, 282–300. doi:10.1177/194008291000300304.	Viverridae	Frugivory
Muñoz-Gallego, R., Fedriani, J. M., and Traveset, A. (2019). Non-native Mammals Are the Main Seed Dispersers of the Ancient Mediterranean Palm *Chamaerops humilis* L. in the Balearic Islands: Rescuers of a Lost Seed Dispersal Service? *Front. Ecol. Evol.* 7, 1–16. doi:10.3389/fevo.2019.00161.	Mustelidae	Seed Dispersal

Citation	Family	Study Focus
Munro, R. H. M. M., Nielsen, S. E., Price, M. H., Stenhouse, G. B., Boyce, M. S., Unro, R. H. M. M., et al. (2006). Seasonal and Diel Patterns of Grizzly Bear Diet and Activity in West-Central Alberta. *J. Mammal.* 87, 1112–1121. doi:10.1644/05-MAMM-A-410R3.1.	Ursidae	Frugivory
Murdoch, J. D., Buyandelger, S., and Cypher, B. L. (2009). Patterns of Seed Occurrence in Corsac and Red Fox Diets in Mongolia. *J. Arid Environ.* 73, 381–384. doi:10.1016/j.jaridenv.2008.10.002.	Canidae	Seed Dispersal
Murdoch, J. D., Munkhzul, T., Buyandelger, S., Reading, R. P., and Sillero-Zubiri, C. (2010). Seasonal Food Habits of Corsac and Red Foxes in Mongolia and the Potential for Competition. *Mamm. Biol.* 75, 36–44. doi:10.1016/j.mambio.2008.12.003.	Canidae	Frugivory
Nagamitsu, T., Shuri, K., Kikuchi, S., Koike, S., Naoe, S., and Masaki, T. (2019). Multiscale Spatial Genetic Structure Within and Between Populations of Wild Cherry Trees in Nuclear Genotypes and Chloroplast Haplotypes. *Ecol. Evol.* 9, 11266–11276. doi:10.1002/ece3.5628.	Ursidae	Seed Dispersal
Nagy-Reis, M. B., Ribeiro, M. C., Setz, E. Z. F., and Chiarello, A. G. (2019). The Key Role of Protection Status in Safeguarding the Ecological Functions of Some Neotropical Mammals. *Biodivers. Conserv.* 28, 2599–2613. doi:10.1007/s10531-019-01783-y.	Mustelidae	Seed Dispersal
Nakabayashi, M., Ahmad, A. H., and Kohshima, S. (2016). Behavioral Feeding Strategy of Frugivorous Civets in a Bornean Rainforest. *J. Mammal.* 97, 798–805. doi:10.1093/jmammal/gyw005.	Viverridae	Frugivory
Nakabayashi, M., Ahmad, A. H., and Kohshima, S. (2017). Fruit Selection of a Binturong (*Arctictis binturong*) By Focal Animal Sampling in Sabah, Malaysian Borneo. *Mammalia* 81, 107–110. doi:10.1515/mammalia-2015-0009.	Viverridae	Frugivory
Nakabayashi, M., Inoue, Y., Ahmad, A. H., and Izawa, M. (2019). Limited Directed Seed Dispersal in the Canopy as One of the Determinants of the Low Hemiepiphytic Figs' Recruitments in Bornean Rainforests. *PLoS One* 14, 1–17. doi:10.1371/journal.pone.0217590.	Viverridae	Seed Dispersal
Nakashima, Y., Inoue, E., Inoue-Murayama, M., and Sukor, J. A. (2010). High Potential of a Disturbance-Tolerant Frugivore, the Common Palm Civet Paradoxurus hermaphroditus (Viverridae), as a Seed Disperser for Large-Seeded Plants. Mammal Study 35, 209–215. doi:10.3106/041.035.0307.	Viverridae	Seed Dispersal
Nakashima, Y., Inoue, E., Inoue-Murayama, M., and Sukor, J. R. A. (2010). Functional Uniqueness of a Small Carnivore as Seed Dispersal Agents: A Case Study of the Common Palm Civets in the Tabin Wildlife Reserve, Sabah, Malaysia. Oecologia 164, 721–730. doi:10.1007/s00442-010-1714-1.	Viverridae	Seed Dispersal

Citation	Family	Study Focus
Naoe, S., Tayasu, I., Sakai, Y., Masaki, T., Kobayashi, K., Nakajima, A., et al. (2016). Mountain-Climbing Bears Protect Cherry Species From Global Warming Through Vertical Seed Dispersal. *Curr. Biol.* 26, R315–R316. doi:10.1016/j.cub.2016.03.002.	Mustelidae, Ursidae	Seed Dispersal
Naoe, S., Tayasu, I., Sakai, Y., Masaki, T., Kobayashi, K., Nakajima, A., et al. (2019). Downhill Seed Dispersal by Temperate Mammals: A Potential Threat to Plant Escape From Global Warming. *Sci. Rep.* 9, 1–11. doi:10.1038/s41598-019-51376-6.	Canidae, Mustelidae, Ursidae	Seed Dispersal
Needham, R., Odden, M., Lundstadsveen, S. K., and Wegge, P. (2014). Seasonal Diets of Red Foxes in a Boreal Forest With a Dense Population of Moose: The Importance of Winter Scavenging. *Acta Theriol. (Warsz).* 59, 391–398. doi:10.1007/s13364-014-0188-7.	Canidae	Frugivory
Nettelbeck, A. R. (1998). Encounters between Lar Gibbons (*Hylobates lar*) and Binturongs (*Arctictis binturong*). *Folia Primatol.* 69, 392–396. doi:10.1159/000021659.	Viverridae	Frugivory
Niederhauser, E. C., and Matlack, G. R. (2015). All Frugivores Are Not Equal: Exploitation Competition Determines Seed Survival and Germination in a Fleshy-Fruited Forest Herb. *Plant Ecol.* 216, 1203–1211. doi:10.1007/s11258-015-0494-4.	Procyonidae	Seed Dispersal
Niederhauser, E. C., and Matlack, G. R. (2017). Do Deer and Raccoons Defecate in the Right Place? Fitness Consequences of Vertebrate Seed Dispersal for a Deciduous Forest Herb. Oecologia 183, 727–737. doi:10.1007/s00442-016-3803-2.	Procyonidae	Seed Dispersal
Niederhauser, E. C., and Matlack, G. R. (2017). Secondary Dispersal of Forest Herb Seeds From Raccoon Dung: Contrasting Service by Multiple Vectors. Plant Ecol. 218, 1135–1147. doi:10.1007/s11258-017-0748-4.	Procyonidae	Seed Dispersal
Novaro, A. J., Walker, R. S., and Suarez, M. (1995). Dry-Season Food Habits of the Gray Fox (*Urocyon cinereoargenteus fraterculus*) in the Belizean Peten. *Mammalia* 59, 19–24. doi:10.1515/mamm.1995.59.1.19.	Canidae	Frugivory
Nowak, J., and Crone, E. E. (2012). It Is Good to Be Eaten by a Bear: Effects of Ingestion on Seed Germination. *Am. Midl. Nat.* 167, 205–209. doi:10.1674/0003-0031-167.1.205.	Ursidae	Seed Dispersal
Noyce, K. V., and Garshelis, D. L. (2011). Seasonal Migrations of Black Bears (*Ursus americanus*): Causes and Consequences. *Behav. Ecol. Sociobiol.* 65, 823–835. doi:10.1007/s00265-010-1086-x.	Ursidae	Frugivory
O'Connor, J. M., Burrows, D. M., Allen, B. L., and Burnett, S. E. (2020). Is the European Red Fox a Vector of the Invasive Basket Asparagus (*Asparagus aethiopicus*) In Eastern Australia? *Aust. Mammal.* 42, 204–210. doi:10.1071/AM19001.	Canidae	Seed Dispersal

Citation	Family	Study Focus
Osorio, C., Muñoz, A., Guarda, N., Bonacic, C., and Kelly, M. (2020). Exotic Prey Facilitate Coexistence Between Pumas and Culpeo Foxes in the Andes of Central Chile. *Diversity* 12. doi:10.3390/D12090317.	Canidae	Frugivory
Osugi, S., Trentin, B. E., and Koike, S. (2019). Impact of Wild Boars on the Feeding Behavior of Smaller Frugivorous Mammals. *Mamm. Biol.* 97, 22–27. doi:10.1016/j.mambio.2019.03.013.	Canidae, Mustelidae, Procyonidae, Viverridae	Frugivory
Osugi, S., Trentin, B. E., and Koike, S. (2020). What Determines the Seedling Viability of Different Tree Species in Raccoon Dog Latrines? *Acta Oecologica* 106, 103604. doi:10.1016/j.actao.2020.103604.	Canidae	Seed Dispersal
Otani, T. (2002). Seed Dispersal by Japanese Marten *Martes melampus* in the Subalpine Shrubland of Northern Japan. *Ecol. Res.* 17, 29–38. doi:10.1046/j.1440-1703.2002.00460.x.	Mustelidae	Seed Dispersal
Page, L. K., Swihart, R. K., and Kazacos, K. R. (1999). Implications of Raccoon Latrines in the Epizootiology of <i>Baylisascariasis. *J. Wildl. Dis.* 35, 474–480. doi:10.7589/0090-3558-35.3.474.	Procyonidae	Frugivory
Page, L. K., Swihart, R. K., and Kazacos, K. R. (2001). Seed Preferences and Foraging by Granivores at Raccoon Latrines in the Transmission Dynamics of the Raccoon Roundworm (*Baylisascaris procyonis*).	Procyonidae	Frugivory
Pandolfi, M., De Marinis, A. M., and Petrov, I. (1996). Fruit as a Winter Feeding Resource in the Diet of Stone Marten (*Martes foina*) in East-Central Italy. *Zeitschrift fur Saugetierkd.* 61, 215–220.	Mustelidae	Frugivory
Pannell, C. M., and Koziol, M. J. (1987). Ecological and Phytochemical Diversity of Arillate Seeds in Aglaia (*Meliaceae*): A Study of Vertebrate Dispersal in Tropical Trees. *Philos. Trans. - R. Soc. London, B* 316, 303–333. doi:10.1098/rstb.1987.0029.	Viverridae	Seed Dispersal
Patrick David, J., Manakadan, R., and Ganesh, T. (2015). Frugivory and Seed Dispersal by Birds and Mammals in the Coastal Tropical Dry Evergreen Forests of Southern India: A Review. *Trop. Ecol.* 56, 41–55.	Canidae, Viverridae	Seed Dispersal
Peña-Egaña, M., Loayza, A. P., and Squeo, F. A. (2018). Are Pulp Consumers Effective Seed Dispersers? Tests With a Large-Seeded Tropical Relict Tree. *Biotropica* 50, 898–907. doi:10.1111/btp.12604.	Canidae, Mephitidae	Seed Dispersal
Pendje, G. (1994). Fruit Consumption and Seed Dispersal by the African Civet (*Civettictis civetta*) in Mayombe, Zaire. *Rev. d'Ecologie (La Terre la Vie)* 49, 107–116.	Viverridae	Seed Dispersal
Perea, R., Delibes, M., Polko, M., Suárez-Esteban, A., and Fedriani, J. M. (2013). Context-Dependent Fruit-Frugivore	Canidae, Mustelidae	Frugivory

Citation	Family	Study Focus
Interactions: Partner Identities and Spatio-Temporal Variations. *Oikos* 122, 943–951. doi:10.1111/j.1600-0706.2012.20940.x.		
Peredo, A., Martínez, D., Rodríguez-Pérez, J., and García, D. (2013). Mammalian Seed Dispersal in Cantabrian Woodland Pastures: Network Structure and Response to Forest Loss. *Basic Appl. Ecol.* 14, 378–386. doi:10.1016/j.baae.2013.05.003.	Canidae, Mustelidae	Seed Dispersal
Pereira, L., Vasques, A., Maia, P., Ramos Pereira, M. J., Fonseca, C., and Matos, M. (2019). Native and Exotic Seed Dispersal by the Stone Marten (Martes foina): Implications for the Regeneration of a Relict Climactic Forest in Central Portugal. *Integr. Zool.* 14, 280–292. doi:10.1111/1749-4877.12362.	Mustelidae	Seed Dispersal
Periago, M. E., Tamburini, D. M., Ojeda, R. A., Cáceres, D. M., and Díaz, S. (2017). Combining Ecological Aspects and Local Knowledge for the Conservation of Two Native Mammals in the Gran Chaco. *J. Arid Environ.* 147, 54–62. doi:10.1016/j.jaridenv.2017.07.017.	Canidae	Frugivory
Pigozzi, G. (1992). Frugivory and Seed Dispersal by the European Badger in a Mediterranean Habitat. *J. Mammal.* 73, 630–639. doi:10.2307/1382035.	Mustelidae	Seed Dispersal
Prigioni, C., Balestrieri, A., Remonti, L., and Cavada, L. (2008). Differential Use of Food and Habitat by Sympatric Carnivores in the Eastern Italian Alps. *Ital. J. Zool.* 75, 173–184. doi:10.1080/11250000701885521.	Canidae, Mustelidae	Frugivory
Quintela, F. M., Iob, G., and Artioli, L. G. S. (2014). Diet of *Procyon cancrivorus* (*Carnivora, Procyonidae*) in Restinga and Estuarine Environments of Southern Brazil. *Iheringia. Série Zool.* 104, 143–149. doi:10.1590/1678-476620141042143149.	Procyonidae	Frugivory
Radović, A., and Kovačić, D. (2010). Diet Composition of the Golden Jackal (*Canis aureus* L.) on the Pelješac Peninsula, Dalmatia, Croatia. *Period. Biol.* 112, 219–224.	Canidae	Frugivory
Ray, J. C., and Sunquist, M. E. (2001). Trophic Relations in a Community of African Rainforest Carnivores. *Oecologia* 127, 395–408. doi:10.1007/s004420000604.	Nandiniidae, Viverridae	Frugivory
Rebein, M., Davis, C. N., Abad, H., Stone, T., del Sol, J., Skinner, N., et al. (2017). Seed Dispersal of *Diospyros virginiana* in the Past and the Present: Evidence for a Generalist Evolutionary Strategy. *Ecol. Evol.* 7, 4035–4043. doi:10.1002/ece3.3008.	Canidae, Procyonidae	Seed Dispersal
Requena-Mullor, J. M., López, E., Castro, A. J., Virgós, E., and Castro, H. (2016). Landscape Influence on the Feeding Habits of European Badger (*Meles meles*) in Arid Spain. *Mammal Res.* 61, 197–207. doi:10.1007/s13364-016-0269-x.	Mustelidae	Frugivory

Citation	Family	Study Focus
Riera, N., Traveset, A., and García, O. (2002). Breakage of Mutualisms by Exotic Species: The Case of *Cneorum tricoccon* L. In the Balearic Islands (Western Mediterranean Sea). *J. Biogeogr.* 29, 713–719. doi:10.1046/j.1365-2699.2002.00719.x.	Mustelidae	Seed Dispersal
Rivas-Romero, J. A., and Soto-Shoender, J. R. (2015). Filling in the Gaps: Evaluating the Use of Camera Traps in the Canopy to Examine Frugivore Visits to *Oreopanax echinops* in the Highlands of Guatemala. *Southwest. Nat.* 60, 366–397. doi:10.1894/0038-4909-60.4.366.	Canidae	Frugivory
Rocha, V. J., Aguiar, L. M., Silva-Pereira, J. E., Moro-Rios, R. F., and Passos, F. C. (2008). Feeding Habits of the Crab-Eating Fox, *Cerdocyon Thous* (*Carnivora: Canidae*), in a Mosaic Area With Native and Exotic Vegetation in Southern Brazil. *Rev. Bras. Zool.* 25, 594–600. doi:10.1590/s0101-81752008000400003.	Canidae	Frugivory
Rode, K. D., and Robbins, C. T. (2000). Why Bears Consume Mixed Diets During Fruit Abundance. *Can. J. Zool.* 78, 1640–1645. doi:10.1139/z00-082.	Ursidae	Frugivory
Roehm, K., and Moran, M. D. (2013). Is the Coyote (*Canis latrans*) A Potential Seed Disperser for the American Persimmon (*Diospyros virginiana*)? *Am. Midl. Nat.* 169, 416–421. doi:10.1674/0003-0031-169.2.416.	Canidae	Seed Dispersal
Rosalino, L. M., Loureiro, F., MacDonald, D. W., and Santos-Reis, M. (2003). Food Digestibility of an Eurasian Badger *Meles meles* With Special Reference to the Mediterranean Region. *Acta Theriol. (Warsz).* 48, 283–288. doi:10.1007/BF03194168.	Canidae, Mustelidae, Viverridae	Frugivory
Rosalino, L. M., Rosa, S., and Santos-Reis, M. (2010). The Role of Carnivores as Mediterranean Seed Dispersers. *Ann. Zool. Fennici* 47, 195–205. doi:10.5735/086.047.0304.	Mustelidae	Frugivory
Rosalino, L. M., and Santos-Reis, M. (2009). Fruit Consumption by Carnivores in Mediterranean Europe. *Mamm. Rev.* 39, 67–78. doi:10.1111/j.1365-2907.2008.00134.x.	Canidae, Herpestidae, Mustelidae, Viverridae	Seed Dispersal
Rost, J., Pons, P., and Bas, J. M. (2012). Seed Dispersal by Carnivorous Mammals Into Burnt Forests: An Opportunity for Non-indigenous and Cultivated Plant Species. *Basic Appl. Ecol.* 13, 623–630. doi:10.1016/j.baae.2012.08.016.	Canidae, Mustelidae	Seed Dispersal
Rubalcava-Castillo, F. A., Sosa-Ramírez, J., Luna-Ruíz, J. J., Valdivia-Flores, A. G., Díaz-Núñez, V., and Íñiguez-Dávalos, L. I. (2020). Endozoochorous Dispersal of Forest Seeds by Carnivorous Mammals in Sierra Fría, Aguascalientes, Mexico. *Ecol. Evol.* 10, 2991–3003. doi:10.1002/ece3.6113.	Canidae, Procyonidae	Seed Dispersal
Sakamoto, Y., and Takatsuki, S. (2015). Seeds Recovered From the Droppings at Latrines of the Raccoon Dog (*Nyctereutes*	Canidae	Seed Dispersal

Citation	Family	Study Focus
procyonoides viverrinus): The Possibility of Seed Dispersal. *Zoolog. Sci.* 32, 157–162. doi:10.2108/zs140107.		
Sandoval-Guillén, P., and Yánez-Moretta, P. (2019). Biological and Ecological Aspects of the Spectacled Bear (*Tremarctos ornatus, Ursidae*) In the Ecuadorean Andean Zone and Conservation Perspectives Under the Landscape Species Approach. *La Granja* 30, 19–27. doi:10.17163/lgr.n30.2019.02.	Ursidae	Frugivory
Santos, E. F., Setz, E. Z. F., and Gobbi, N. (2003). Diet of the Maned Wolf (*Chrysocyon brachyurus*) And Its Role in Seed Dispersal on a Cattle Ranch in Brazil. *J. Zool.* 260, 203–208. doi:10.1017/S0952836903003650.	Canidae	Seed Dispersal
Sathyakumar, S., and Viswanath, S. (2003). Observations on Food Habits of Asiatic Black Bear in Kedarnath Wildlife Sanctuary, India: Preliminary Evidence on Their Role in Seed Germination and Dispersal. *Ursus (Knoxville)* 14, 99–103.	Ursidae	Frugivory
Schrecengost, J. D., Kilgo, J. C., Mallard, D., Ray, H. S., and Miller, K. V (2008). Seasonal Food Habits of the Coyote in the South Carolina Coastal Plain. *Southeast. Nat.* 7, 135–144.	Canidae	Frugivory
Selwyn, M., Garrote, P. J., Castilla, A. R., and Fedriani, J. M. (2020). Interspecific Interactions Among Functionally Diverse Frugivores and Their Outcomes for Plant Reproduction: A New Approach Based on Camera-Trap Data and Tailored Null Models. *PLoS One* 15, 1–21. doi:10.1371/journal.pone.0240614.	Canidae	Seed Dispersal
Shakeri, Y. N., White, K. S., and Levi, T. (2018). Salmon-Supported Bears, Seed Dispersal, and Extensive Resource Subsidies to Granivores. *Ecosphere* 9, 1–13. doi:10.1002/ecs2.2297.	Ursidae	Seed Dispersal
Silva, S. I., Bozinovic, F., and Jaksic, F. M. (2005). Frugivory and Seed Dispersal by Foxes in Relation to Mammalian Prey Abundance in a Semiarid Thornscrub. *Austral Ecol.* 30, 739–746. doi:10.1111/j.1442-9993.2005.01449.x.	Canidae	Seed Dispersal
da Silva, F. R., Begnini, R. M., Lopes, B. C., and Castellani, T. T. (2011). Seed Dispersal and Predation in the Palm *Syagrus romanzoffiana* on Two Islands With Different Faunal Richness, Southern Brazil. *Stud. Neotrop. Fauna Environ.* 46, 163–171. doi:10.1080/01650521.2011.617065.	Procyonidae	Seed Dispersal
Silverstein, R. P. (2005). Germination of Native and Exotic Plant Seeds Dispersed by Coyotes (*Canis latrans*) in Southern California. *Southwest. Nat.* 50, 472–478. doi:10.1894/0038-4909(2005)050[0472:GONAEP]2.0.CO;2.	Canidae	Seed Dispersal
Sovada, M. A., Roy, C. C., and Telesco, D. J. (2001). Seasonal Food Habits of Swift Fox (*Vulpes velox*) In Cropland and Rangeland	Canidae	Frugivory

Citation	Family	Study Focus
Landscapes in Western Kansas. *Am. Midl. Nat.* 145, 101–111. doi:10.1674/0003-0031(2001)145[0101:SFHOSF]2.0.CO;2.		
Spennemann, D. H. R. (2018). Review of the Vertebrate-Mediated Dispersal of the Date Palm, *Phoenix dactylifera*. *Zool. Middle East* 64, 283–296. doi:10.1080/09397140.2018.1514785.	Canidae, Ursidae	Seed Dispersal
Spennemann, D. H. R. (2019). The Connective Potential of Vertebrate Vectors Responsible for the Dispersal of the Canary Island Date Palm (*Phoenix canariensis*). *Flora Morphol. Distrib. Funct. Ecol. Plants* 259, 151468. doi:10.1016/j.flora.2019.151468.	Canidae	Seed Dispersal
Spennemann, D. H. R. (2020). The Role of Canids in the Dispersal of Commercial and Ornamental Palm Species. *Mammal Res.* doi:10.1007/s13364-020-00535-6.	Canidae	Seed Dispersal
Sreekumar, P. G., and Balakrishnan, M. (2002). Seed Dispersal by the Sloth Bear (*Melursus ursinus*) in South India. *Biotropica* 34, 474. doi:10.1646/0006-3606(2002)034[0474:sdbtsb]2.0.co;2.	Ursidae	Seed Dispersal
Steinmetz, R., Garshelis, D. L., Chutipong, W., and Seuaturien, N. (2013). Foraging Ecology and Coexistence of Asiatic Black Bears and Sun Bears in a Seasonal Tropical Forest in Southeast Asia. *J. Mammal.* 94, 1–18. doi:10.1644/11-MAMM-A-351.1.	Ursidae	Frugivory
Stevens, M. T., Houghton, S., and Veltkamp, H. A. (2020). Frugivory by Coyotes Decreases the Time to Germination and Increases the Growth of Netleaf Hackberry (*Celtis reticulata*) Seedlings. *Forests* 11, 7–14. doi:10.3390/F11070727.	Canidae	Seed Dispersal
Steyaert, S. M. J. G., Frank, S. C., Puliti, S., Badia, R., Arnberg, M. P., Beardsley, J., et al. (2018). Special Delivery: Scavengers Direct Seed Dispersal Towards Ungulate Carcasses. *Biol. Lett.* 14, 10–13. doi:10.1098/rsbl.2018.0388.	Canidae	Seed Dispersal
Stricklan, D., Saud, P., Cibils, A. F., Steiner, R. L., Cram, D. S., Young, K., et al. (2020). Germination of One-Seed Juniper Seeds Distributed by Different Frugivore Groups. *Rangel. Ecol. Manag.* 73, 433–440. doi:10.1016/j.rama.2019.12.006.	Canidae	Seed Dispersal
Suárez-Esteban, A., Delibes, M., and Fedriani, J. M. (2013). Barriers or Corridors? The Overlooked Role of Unpaved Roads in Endozoochorous Seed Dispersal. J. Appl. Ecol. 50, 767–774. doi:10.1111/1365-2664.12080.	Canidae, Mustelidae	Seed Dispersal
Suárez-Esteban, A., Delibes, M., and Fedriani, J. M. (2013). Unpaved Road Verges as Hotspots of Fleshy-Fruited Shrub Recruitment and Establishment. Biol. Conserv. 167, 50–56. doi:10.1016/j.biocon.2013.07.022.	Canidae, Mustelidae	Seed Dispersal
Subrata, S. A., and Syahbudin, A. (2016). Common Palm Civet as a Potential Seed Disperser of Important Plant Species in Java. *AIP Conf. Proc.* 1744. doi:10.1063/1.4953527.	Viverridae	Seed Dispersal

Citation	Family	Study Focus
Takahashi, K., Shiota, T., Tamatani, H., Koyama, M., Washitani, I., Takahashi, N. K., et al. (2008). Seasonal Variation in Fleshy Fruit Use and Seed Dispersal by the Japanese Black Bear (*Ursus thibetanus japonicus*). *Ecol. Res.* 23, 471–478. doi:10.1007/s11284-007-0382-z.	Ursidae	Seed Dispersal
Takatsuki, S. (2017). Food Habits of the Raccoon Dog at the Tsuda University's Kodaira Campus, Western Tokyo. *Humans Nat.* 28, 1–9.	Canidae	Frugivory
Takatsuki, S., Miyaoka, R., and Sugaya, K. (2018). A Comparison of Food Habits between Japanese Marten and Raccoon Dog in Western Tokyo with Reference to Fruit Use. *Zoolog. Sci.* 35, 68–74. doi:10.2108/zs170116.	Canidae, Mustelidae	Frugivory
Traveset, A. (1995). Seed Dispersal of *Cneorum tricoccon* L. (*Cneoraceae*) By Lizards and Mammals in the Balearic Islands. *Acta Oecologica* 16, 171–178.	Mustelidae, Viverridae	Seed Dispersal
Traveset, A. (2002). Consequences of the Disruption of Plant-Animal Mutualisms for the Distribution of Plant Species in the Balearic Islands. *Rev. Chil. Hist. Nat.* 75, 117–126. doi:10.4067/s0716-078x2002000100011.	Mustelidae, Viverridae	Seed Dispersal
Traveset, A., Bermejo, T., and Willson, M. (2001). Effect of Manure Composition on Seedling Emergence and Growth of Two Common Shrub Species of Southeast Alaska. *Plant Ecol.* 155, 29–34. doi:10.1023/A:1013282313035.	Ursidae	Seed Dispersal
Traveset, A., Escribano-Avila, G., Gómez, J. M., and Valido, A. (2019). Conflicting Selection on *Cneorum tricoccon* (*Rutaceae*) Seed Size Caused by Native and Alien Seed Dispersers. *Evolution (N. Y).* 73, 2204–2215. doi:10.1111/evo.13852.	Mustelidae	Seed Dispersal
Traveset, A., Riera, N., and Mas, R. E. (2017). Ecology of Fruit-Colour Polymorphism in *Myrtus communis* and Differential Effects of Birds and Mammals on Seed Germination and Seedling Growth. 89, 749–760.	Mustelidae	Seed Dispersal
Traveset, A., and Willson, M. F. (1997). Effect of Birds and Bears on Seed Germination of Fleshy-Fruited Plants in Temperate Rainforests of Southeast Alaska. *Oikos* 80, 89. doi:10.2307/3546519.	Ursidae	Seed Dispersal
Traveset, A., and Willson, M. F. (1998). Ecology of the Fruit-Colour Polymorphism in *Rubus spectabilis*. *Evol. Ecol.* 12, 331–345. doi:10.1023/A:1006504317585.	Ursidae	Seed Dispersal
Tsang, A. C. W., and Corlett, R. T. (2005). Reproductive biology of the *Ilex* species (*Aquifoliaceae*) in Hong Kong, China. *Can. J. Bot.* 83, 1645–1654. doi:10.1139/b05-131.	Viverridae	Seed Dispersal

Citation	Family	Study Focus
Tsuji, Y., Konta, T., Akbar, M. A., and Hayashida, M. (2020). Effects of Japanese Marten (Martes melampus) Gut Passage on Germination of Actinidia arguta (Actinidiaceae): Implications for Seed Dispersal. Acta Oecologica 105, 103578. doi:10.1016/j.actao.2020.103578.	Mustelidae	Seed Dispersal
Tsuji, Y., Miura, S., Kotoge, T., Shiraishi, T., and Murai, H. (2015). Effects of Food Intake on Digesta Passage Time in Captive Japanese Martens (*Martes melampus*) and Implications for Endozoochorous Seed Dispersal. *Mammal Study* 40, 13–18. doi:10.3106/041.040.0103.	Mustelidae	Seed Dispersal
Tsuji, Y., Okumura, T., Kitahara, M., and Jiang, Z. (2016). Estimated Seed Shadow Generated by Japanese Martens(*Martes melampus*): Comparison with Forest-Dwelling Animals in Japan. *Zoolog. Sci.* 33, 352–357. doi:10.2108/zs160017.	Mustelidae	Seed Dispersal
Tsuji, Y., Shiraishi, T., and Miura, S. (2011). Gastrointestinal Passage Time of Seeds Ingested by Captive Japanese Martens Martes melampus. Acta Theriol. (Warsz). 56, 353–357. doi:10.1007/s13364-011-0034-0.	Mustelidae	Seed Dispersal
Tsuji, Y., Tatewaki, T., and Kanda, E. (2011). Endozoochorous Seed Dispersal by Sympatric Mustelids, Martes melampus and Mustela itatsi, in Western Tokyo, Central Japan. Mamm. Biol. 76, 628–633. doi:10.1016/j.mambio.2011.01.002.	Mustelidae	Seed Dispersal
Tsuji, Y., Yanti, R., Takizawa, A., and Hagiwara, T. (2020). Interspecific Difference in Seed Dispersal Characteristics Between Japanese Macaques (Macaca fuscata) and Sympatric Japanese Martens (Martes Melampus). Folia Primatol. 8580, 711–720. doi:10.1159/000509385.	Mustelidae	Seed Dispersal
Tsuji, Y., Yasumoto, Y., and Takatsuki, S. (2014). Multi-Annual Variation in the Diet Composition and Frugivory of the Japanese Marten (*Martes melampus*) In Western Tokyo, Central Japan. *Acta Theriol. (Warsz).* 59, 479–483. doi:10.1007/s13364-014-0181-1.	Mustelidae	Frugivory
Varela, O., and Bucher, E. H. (2006). Passage Time, Viability, and Germination of Seeds Ingested by Foxes. *J. Arid Environ.* 67, 566–578. doi:10.1016/j.jaridenv.2006.03.013.	Canidae	Seed Dispersal
Varela, O., Cormenzana-Méndez, A., Krapovickas, L., and Bucher, E. H. (2008). Seasonal diet of the pampas fox (Lycalopex gymnocercus) in the chaco dry woodland, northwestern Argentina. *J. Mammal.* 89, 1012–1019. doi:10.1644/07-MAMM-A-125.1.	Canidae	Frugivory
Vasconcellos-Neto, J., de Albuquerque, L. B., and Silva, W. R. (2009). Seed dispersal of *Solanum thomasiifolium* Sendtner (*Solanaceae*) in the Linhares Forest, Espírito Santo state, Brazil.	Canidae	Seed Dispersal

Citation	Family	Study Focus
Acta Bot. Brasilica 23, 1171–1179. doi:10.1590/s0102-33062009000400027.		
Vergara-Tabares, D. L., Whitworth-Hulse, J. I., and Funes, G. (2018). Germination Response of *Lithraea molleoides* Seeds Is Similar After Passage Through the Guts of Several Avian and a Single Mammalian Disperser. *Botany* 96, 485–490. doi:10.1139/cjb-2017-0232.	Canidae	Seed Dispersal
Vieira, E. M., and Port, D. (2007). Niche Overlap and Resource Partitioning Between Two Sympatric Fox Species in Southern Brazil. *J. Zool.* 272, 57–63. doi:10.1111/j.1469-7998.2006.00237.x.	Canidae	Frugivory
Virgós, E., Cabezas-Díaz, S., Mangas, J. G., and Lozano, J. (2010). Spatial Distribution Models in a Frugivorous Carnivore, the Stone Marten (*Martes foina*): Is the Fleshy-Fruit Availability a Useful Predictor? *Anim. Biol.* 60, 423–436. doi:10.1163/157075610X523297.	Mustelidae	Frugivory
Vynne, C., and Kinsella, J. M. (2009). First Record of Entodiniomorph Ciliates in a Carnivore, the Maned Wolf (*Chrysocyon brachyurus*), From Brazil. *J. Zoo Wildl. Med.* 40, 382–384. doi:10.1638/2008-0119.1.	Canidae	Frugivory
Wang, W., Ma, J., Yu, H., and Hu, L. (2008). Food Habits of Asiatic Black Bears in the Xiao Xing' Anling Mountains. *Acta Theriol. Sin.* 28, 7–13.	Ursidae	Frugivory
Weinstein, S. B., Moura, C. W., Mendez, J. F., and Lafferty, K. D. (2018). Fear of Feces? Tradeoffs Between Disease Risk and Foraging Drive Animal Activity Around Raccoon Latrines. *Oikos* 127, 927–934. doi:10.1111/oik.04866.	Procyonidae	Frugivory
Welch, C. A., Keay, J., Kendall, K. C., and Robbins, C. T. (1997). Constraints on Frugivory by Bears. *Ecology* 78, 1105–1119. doi:10.1890/0012-9658(1997)078[1105:COFBB]2.0.CO;2.	Ursidae	Frugivory
Wiegand, T., Dean, W. R. J., and Milton, S. J. (1997). Simulated Plant Population Responses to Small-Scale Disturbances in Semi-arid Shrublands. *J. Veg. Sci.* 8, 163–176. doi:10.2307/3237345.	Canidae	Seed Dispersal
Willson, M. F. (1993). Mammals as Seed Dispersal Mutualist in North America. *Oikos* 67, 159–176.	Canidae, Mephitidae, Mustelidae, Procyonidae, Ursidae	Frugivory
Willson, M. F., and Gende, S. M. (2004). Seed dispersal by Brown Bears, Ursus arctos, in Southeastern Alaska. *Can. Field-Naturalist* 118, 499–503. doi:10.22621/cfn.v118i4.53.	Ursidae	Seed Dispersal
Wright, S. J., Carrasco, C., Calderón, O., and Paton, S. (1999). The El Nino Southern Oscillation, Variable Fruit Production, and	Procyonidae	Frugivory

Citation	Family	Study Focus
Famine in a Tropical Forest. *Ecology* 80, 1632–1647. doi:10.1890/0012-9658(1999)080[1632:TENOSO]2.0.CO;2.		
Xu Li, Jiang Zhaowen, Ma Yiqing, Jin Ailian, Wang Yongqing, and Buskirk, S. W. (1996). Winter Food Habits of Sable (*Martes zibellina*) in Daxinganling Mountains, China. *Acta Theriol. Sin.* 16, 272–277.	Mustelidae	Frugivory
Yasumoto, Y., and Takatsuki, S. (2015). The Japanese Marten Favors *Actinidia arguta*, a Forest Edge Liane as a Directed Seed Disperser. *Zoolog. Sci.* 32, 255–259. doi:10.2108/zs140241.	Mustelidae	Seed Dispersal
Zagainova, O. S., and Markov, N. I. (2011). The Diet of Asian Badger, *Meles leucurus* Hodgson, 1847, in Samarovskii Chugas Nature Park, Western Siberia. *Russ. J. Ecol.* 42, 414–420. doi:10.1134/S1067413611050158.	Mustelidae	Frugivory
Zhang, H., and Chu, L. M. (2013). Seed Rain and Seedling Survival Are Major Factors Limiting Vegetation Regeneration on Rehabilitated Quarries. *Landsc. Ecol. Eng.* 11, 29–38. doi:10.1007/s11355-013-0231-x.	Viverridae	Seed Dispersal
Zhou, Y. B., Newman, C., Buesching, C. D., Zalewski, A., Kaneko, Y., MacDonald, D. W., et al. (2011). Diet of an Opportunistically Frugivorous Carnivore, *Martes flavigula*, in Subtropical Forest. *J. Mammal.* 92, 611–619. doi:10.1644/10-MAMM-A-296.1.	Mustelidae	Seed Dispersal
Zhou, Y., Newman, C., Chen, J., Xie, Z., and Macdonald, D. W. (2013). Anomalous, Extreme Weather Disrupts Obligate Seed Dispersal Mutualism: Snow in a Subtropical Forest Ecosystem. Glob. Chang. Biol. 19, 2867–2877. doi:10.1111/gcb.12245.	Mustelidae	Seed Dispersal
Zhou, Y., Newman, C., Xie, Z., and MacDonald, D. W. (2013). Peduncles Elicit Large-Mammal Endozoochory in a Dry-Fruited Plant. Ann. Bot. 112, 85–93. doi:10.1093/aob/mct096.	Mustelidae	Frugivory
Zhou, Y. B., Slade, E., Newman, C., Wang, X. M., and Zhang, S. Y. (2008). Frugivory and Seed Dispersal by the Yellow-Throated Marten, Martes flavigula, in a Subtropical Forest of China. J. Trop. Ecol. 24, 219–223. doi:10.1017/S0266467408004793.	Mustelidae, Ursidae, Viverridae	Seed Dispersal
Zhou, Y. B., Zhang, L., Kaneko, Y., Newman, C., and Wang, X. M. (2008). Frugivory and Seed Dispersal by a Small Carnivore, the Chinese Ferret-Badger, Melogale moschata, in a Fragmented Subtropical Forest of Central China. For. Ecol. Manage. 255, 1595–1603. doi:10.1016/j.foreco.2007.11.018.	Mustelidae, Ursidae, Viverridae	Seed Dispersal
Zulkarnaen, R. N., Nisyawati, and Witono, J. R. (2020). The Growth and Distribution Pattern of Endemic Java Palm (*Pinanga javana* Blume) in Mt. Slamet, Central Java, Indonesia. *AIP Conf. Proc.* 2231. doi:10.1063/5.0002814.	Viverridae	Seed Dispersal

Citation	Family	Study Focus
	Family	Study Focus
Acevedo Quintero, J. F., and Zamora-Abrego, J. G. (2016). Role of Mammals on Seed Dispersal and Predation Processes of Mauritia Flexuosa (*Arecaceae*) In the Colombian Amazon. *Rev. Biol. Trop.* 64, 5. doi:10.15517/rbt.v64i1.18157.	Canidae	Seed Dispersal

Supplemental Table 2. Seach terms used in literature search. All searches utilized a term pair with one term from the Plant/Dispersal column and one from the *Carnivoran* column.

Plant/Dispersal Search Term	*Carnivoran* Search Term		
	General terms	Family	Genus
Seed dispersal	Carnivore	*Viverridae*	
frugivory	*Carnivora*		*Arctictis*
long-distance dispersal	Bear		*Arctogalidia*
seed	wolf		*Macrogalidia*
	fox		*Paguma*
	coyote		*Paradoxurus*
	badger		*Chrotogale*
	hyaena		*Cynogale*
	polecat		*Diplogale*
	fisher		*Hemigalus*
	raccoon		*Prionodon*
	weasel		*Civettictis*
			Genetta
			Poiana
			Viverra
			Viverricula
		Eupleridae	
			Cryptoprocta
			Eupleres
			Fossa
			Galidia
			Galidictis
			Mungotictis
			Salanoia
		Nandiniidae	
			Nandinia
		Hyaenidae	
			Crocuta
			Hyaena
			Proteles
		Canidae	
			Atelocynus
			Canis
			Cerdocyon
			Chrysocyon
			Cuon
			Dusicyon
			Lycalopex

Plant/Dispersal Search Term	*Carnivoran* Search Term		
	General terms	Family	Genus
			Lycaon
			Nyctereutes
			Otocyon
			Speothos
			Urocyon
			Vulpes
		Ursidae	
			Ailuropoda
			Helarctos
			Melursus
			Tremarctos
			Ursus
		Mustelidae	
			Aonyx
			Enhydra
			Hydrictis
			Lontra
			Lutra
			Lutrogale
			Pteronura
			Arctonyx
			Eira
			Galictis
			Gulo
			Ictonyx
			Lyncodon
			Martes
			Meles
			Mellivora
			Melogale
			Mustela
			Neovison
			Poecilogale
			Taxidea
			Vormela
		Mephitidae	
			Conepatus
			Mephitis
			Mydaus
			Spilogale

Plant/Dispersal Search Term	*Carnivoran* Search Term		
	General terms	Family	Genus
		Procyonidae	
			Bassaricyon
			Bassariscus
			Nasua
			Nasuella
			Potos
			Procyon
		Ailuridae	
			Ailurus

Supplemental Table 3. We conducted a literature search outlined in box 1, within the main manuscript. The search yielded 280 peer-reviewed publications that observed or discussed *Carnivoran* consumption of fruit and seed. Plants identified in these studies belonged to 118 different plant families and were identified to genera and species in most cases. This table displays the count of unique genera and species identified in the literature; blank cells indicate that the taxa were only identified to the next higher taxonomic level.

Family	Count of Genera	Count of Species
Rosaceae	27	96
Arecaceae	22	27
Lauraceae	16	19
Anacardiaceae	13	21
Moraceae	12	52
Myrtaceae	12	19
Euphorbiaceae	12	13
Rubiaceae	12	11
Annonaceae	10	17
Sapotaceae	10	12
Rutaceae	10	11
Sapindaceae	10	9
Ericaceae	9	27
Araliaceae	9	14
Solanaceae	8	14
Oleaceae	8	11
Cucurbitaceae	8	7
Liliaceae	8	4
Rhamnaceae	7	21
Vitaceae	7	10
Burseraceae	7	9
Araceae	7	3
Malvaceae	6	7
Asparagaceae	6	6
Cactaceae	6	6
Myristicaceae	6	6
Cornaceae	5	12
Celastraceae	5	9
Melastomataceae	5	8
Berberidaceae	5	6
Fabaceae	5	6
Menispermaceae	5	5
Santalaceae	5	5

Family	Count of Genera	Count of Species
Ebenaceae	4	15
Caprifoliaceae	4	9
Meliaceae	4	8
Clusiaceae	4	6
Lardizabalaceae	4	6
Taxaceae	4	6
Urticaceae	4	6
Apocynaceae	4	4
Lamiaceae	4	4
Salicaceae	4	4
Adoxaceae	3	16
Elaeagnaceae	3	8
Bromeliaceae	3	5
Verbenaceae	3	4
Dilleniaceae	3	2
Aquifoliaceae	2	11
Cupressaceae	2	11
Ulmaceae	2	8
Symplocaceae	2	6
Boraginaceae	2	5
Cannabaceae	2	5
Elaeocarpaceae	2	5
Loganiaceae	2	5
Magnoliaceae	2	5
Musaceae	2	5
Myricaceae	2	5
Schisandraceae	2	5
Capparaceae	2	4
Passifloraceae	2	4
Phytolaccaceae	2	4
Pentaphylacaceae	2	3
Primulaceae	2	3
Thymelaeaceae	2	3
Bignoniaceae	2	2
Chrysobalanaceae	2	2
Loranthaceae	2	2
Malpighiaceae	2	2
Olacaceae	2	2

Family	Count of Genera	Count of Species
Palmae	2	2
Poaceae	2	2
Ranunculaceae	2	2
Sabiaceae	2	2
Zygophyllaceae	2	2
Coriariaceae	2	1
Actinidiaceae	1	6
Elaenacnaceae	1	4
Grossulariaceae	1	4
Smilacaceae	1	4
Convolvulaceae	1	3
Gnetaceae	1	3
Pandanaceae	1	3
Ephedraceae	1	2
Piperaceae	1	2
Polygonaceae	1	2
Achariaceae	1	1
Amaranthaceae	1	1
Apiaceae	1	1
Asteraceae	1	1
Caricaceae	1	1
Dioscoreaceae	1	1
Ginkgoaceae	1	1
Goodeniaceae	1	1
Helwingiaceae	1	1
Hydnoraceae	1	1
Muntingiaceae	1	1
Orchidaceae	1	1
Papaveraceae	1	1
Plantaginaceae	1	1
Podocarpaceae	1	1
Putranjivaceae	1	1
Resedaceae	1	1
Salvadoraceae	1	1
Scrophulariaceae	1	1
Stachyuraceae	1	1
Theaceae	1	1
Zingiberaceae	1	1

Family	Count of Genera	Count of Species
Connaraceae	1	
Monimiaceae	1	
Nyssaceae	1	
Styracaceae	1	
Combretaceae		
Guttiferae		
Icacinaceae		
Lecythidaceae		
Lythraceae		

Supplemental Table 4. The number of documented seed *Carnivoran* relationships effect on seed breakage, viability, and germination (papers are listed in decending order based on the number of seed species viability reported, with papers listing only seed breakage at the end). Each parenthetical citation references a citation from Supplemental Table 2. Seed breakage information describes the totality of fates for seeds in the respective study. Viability is reported as the number of seed *Carnivoran* pairings, as either increasing or decreasing viability for studies that had an undigested seed lot control to compare too, or as viable seeds documented when post gut passage viability was reported without a control comparison. Three categories of germination are reported as the number of seed *Carnivoran* pairings, no change in germination, increase or accelerated germination, and decrease or delayed germination. Studies reporting germination used both increased and accelerated language and as a minority of studies further explored viability after germination it is not possible to broadly state how germination was affected outside of the temporal confines of each study.

	Seed Breakage	Decrease Viability	Maintain Viability	Viable Seeds Documented	No change in Germination	Increase/ accelerate Germination	Decrease/ delay Germination
(Karimi et al. 2020)				33			
(Fahimi et al. 2018)				33			
(Nakashima et al. 2010b)				32			
(Mudappa et al. 2010)				14			
(Periago et al. 2017)		2		8			
(Traveset and Willson 1997)				6	5	1	
(Matías et al. 2010)				6			
(Varela and Bucher 2006)	90-99.9% Intact			4		4	
(Colon and Campos-Arceiz 2013)				3	2		1
(Cypher and Cypher 1999)		1		2	1	1	1
(Helbig-bonitz et al. 2013)				3		3	
(Nowak and Crone 2012)				3		3	
(Rebein et al. 2017)				2		2	
(Silverstein 2005)				2		1	1

	Seed Breakage	Decrease Viability	Maintain Viability	Viable Seeds Documented	No change in Germination	Increase/ accelerate Germination	Decrease/ delay Germination
(Tsuji et al. 2020a)				1	1		
(Amodeo et al. 2017)		1			1		
(Borchert and Tyler 2011)			1			1	
(Campos and Ojeda 1997)				1	1		
(Cancio et al. 2016)			1			1	
(Enders and Vander Wall 2012)				1			1
(Farris et al. 2017)				1	1		
(Furubayashi 2008)	No Seed Breakage			1		1	
(Juan et al. 2006)				1		1	
(Kulavmode et al. 2015)				1			1
(Lima et al. 2015)			1		1		
(Maldonado et al. 2018)				1	1		
(Milton and Dean 2001)				1		1	
(Morales-Paredes et al. 2015)			1				1
(Niederhauser and Matlack 2015)				1	1		
(Roehm and Moran 2013)			1		1		
(Sathyakumar and Viswanath 2003)			1			1	
(Stevens et al. 2020)				1		1	
(Stricklan et al. 2020)				1		1	
(Traveset et al. 2019)				1		1	
(Traveset et al. 2017)				1	1		
(Vasconcellos-Neto et al. 2009)			1				1
(Vergara-Tabares et al. 2018)			1			1	

	Seed Breakage	Decrease Viability	Maintain Viability	Viable Seeds Documented	No change in Germination	Increase/ accelerate Germination	Decrease/ delay Germination
(Lautenschlager 1997)			1		1		
(Fedriani and Delibes 2011)		1					
(Hewitt and Miyanishi 1997)				1			
(Koike et al. 2012)				1			
(Fedriani and Delibes 2009b)	>90% Intact						
(Pigozzi 1992)	91-99% Intact						
(Suárez-Esteban et al. 2013a)	98.2% Intact						
(Zhou et al. 2013b)	99% Intact						
(Lalleroni et al. 2017)	Acorns Crushed Small Seeds Intact						
(Aronne and Russo 1997)	No Seed Breakage						
(Grünewald et al. 2010)	No Seed Breakage						
(Tsuji et al. 2020b)	No Seed Breakage						
(Zhou et al. 2008b)	No Seed Breakage						
(González-Varo et al. 2013)	No Seed Mimics Broken						
(Herrera et al. 2016)	No Seed Mimics Broken						
(Mise et al. 2016)	No Seed Mimics Broken						
(Murdoch et al. 2009)	99% Intact						

	Seed Breakage	Decrease Viability	Maintain Viability	Viable Seeds Documented	No change in Germination	Increase/ accelerate Germination	Decrease/ delay Germination
(Koike et al. 2008)	Nuts and Dry Fruit Damaged, Small seeds 97+% Intact						
Totals		5	12	167	19	25	7

Supplemental Table 5. Animal body mass (Mass, kg), home range (minimum convex polygon, km^2) and gut-passage time (Gut-passage time, hours), and the range of gut-passage time of *Carnivoran* species identified as frugivores/seed dispersers. All values are for adults of both sexes unless noted otherwise. All reported gut-passage times are for mixed or pure fruit diets. Species with multiple records in Smith et al. 2003 are reported as a mean of the data included therein. All values were used to analyze the relationship between mass and home range, and mass and gut-passage time, except *Ursus arctos*, were removed from the gut-passage time analysis due to being an extreme outlier, and relying on gut-passage data from a strictly fruit-based experimental diet in captivity.

Family	Genus	Species	Mass	Home range size	Gut-passage time	Gut-passage time range	Data Source
Procyonidae	*Potos*	*flavus*	3.00	0.28	2.50	0.7-5.6	1, 2, 3
Mustelidae	*Martes*	*melampus*	1.00	2.68	5.50	0.6-51.7	1, 4, 5
Mustelidae	*Martes*	*americana*	1.25	7.07	4.30	3.8-10.3	1, 2, 6
Ursidae	*Ursus*	*arctos*	180.52	810.46	5.78	4.6-7.0*	1, 2, 7
Viverridae	*Arctictis*	*binturong*	9.88	6.20**	6.50	3.3-9.3	1, 3, 8
Canidae	*Lycalopex*	*gymnocercus*	4.54	+	6.80	5.5-8.1	9, 10
Canidae	*Cerdocyon*	*thous*	5.24	3.00	7.70	4.5-13.0	1, 2, 11
Canidae	*Nyctereutes*	*procyonoides*	4.04	2.52	8.83	4-32.8	1, 2, 11
Canidae	*Canis*	*latrans*	13.41	28.58	14.82	2.0-36.0	1, 2, 12
Ursidae	*Ursus*	*thibetanus*	77.50	12.56	18.90	3.2-44.3	1, 13, 14
Mustelidae	*Mustela*	*nivalis*	0.10	0.65	-	-	1, 2
Mustelidae	*Mustela*	*erminea*	0.12	1.32	-	-	1, 2
Mustelidae	*Mustela*	*frenata*	0.15	0.18	-	-	1, 2
Herpestidae	*Herpestes*	*javanicicus*	0.43	0.03	-	-	2, 2
Mustelidae	*Mustela*	*furo*	0.81	0.90	-	-	2, 2
Mephitidae	*Spilogale*	*putorius*	0.92	0.23	-	-	1, 2
Procyonidae	*Bassariscus*	*astutus*	1.13	0.83	-	-	1, 2
Mephitidae	*Conepatus*	*semistriatus*	1.20	0.36	-	-	1, 2
Mustelidae	*Martes*	*martes*	1.30	9.09	-	-	1, 2
Herpestidae	*Herpestes*	*edwardsi*	1.30	3.10	-	-	7, 2
Mephitidae	*Conepatus*	*humboldti*	1.32	0.16	-	-	2, 2
Mustelidae	*Martes*	*foina*	1.54	4.36	-	-	1, 2
Viverridae	*Genetta*	*genetta*	1.80	7.81	-	-	1, 2
Canidae	*Chrysocyon*	*brachyurus*	1.85	27.03	-	-	1, 2
Canidae	*Urocyon*	*littoralis*	1.90	0.19	-	-	1, 2
Mephitidae	*Mephitis*	*mephitis*	2.09	2.98	-	-	1, 2
Viverridae	*Genetta*	*tigrina*	2.23	0.06	-	-	1, 2
Herpestidae	*Herpestes*	*naso*	3.00	0.52	-	-	1, 2
Viverridae	*Paradoxuru*	*hermaphroditus*	3.16	5.32	-	-	1, 2
Canidae	*Vulpes*	*ruppelli*	3.25	30.40	-	-	2, 2
Mustelidae	*Martes*	*pennanti*	4.00	16.76	-	-	1, 2
Procyonidae	*Nasua*	*narica*	4.03	1.73	-	-	1, 2

Canidae	*Otocyon*	*megalotus*	4.15	3.53	-	-	2, 2
Viverridae	*Paguma*	*larvata*	4.30	3.70	-	-	1, 2
Mustelidae	*Eira*	*barbata*	4.47	14.62	-	-	2, 2
Canidae	*Vulpes*	*macroti*	4.50	8.77	-	-	2, 2
Canidae	*Urocyon*	*cinereoargeneu*	4.54	2.74	-	-	2, 2
Ailuridae	*Ailurus*	*fulgens*	4.90	1.02	-	-	1, 2
Herpestidae	*Herpestes*	*ichneumon*	5.17	2.80	-	-	1, 2
Canidae	*Vulpes*	*vulpes*	5.48	4.92	-	-	1, 2
Procyonidae	*Procyon*	*lotor*	5.52	3.30	-	-	1, 2
Canidae	*Canis*	*mesomelas*	8.50	15.80	-	-	1, 2
Viverridae	*Viverra*	*zibetha*	9.50	12.00	-	-	1, 2
Canidae	*Canis*	*adustus*	10.25	1.10	-	-	1, 2
Canidae	*Canis*	*aureus*	10.35	1.47	-	-	1, 2
Mustelidae	*Meles*	*meles*	13.00	2.18	-	-	1, 2
Canidae	*Cuon*	*alpinus*	14.17	68.75	-	-	1, 2
Canidae	*Canis*	*simensi*	27.75	5.39	-	-	2, 2
Canidae	*Canis*	*lupus*	32.18	468.04	-	-	1, 2
Hyaenidae	*Hyaena*	*hyaena*	41.71	59.45	-	-	1, 2
Ursidae	*Melursus*	*ursinus*	93.13	10.00	-	-	1, 2
Ursidae	*Ursus*	*americanus*	99.95	39.27	-	-	1, 2

Table sources: 1. Smith et al. 2003, 2. Kelt and Van Vuren 2001, 3. Lambert et al. 2014, 4. Tsuji et al. 2016, 5. Tsuji et al. 2015, 6. Hickey et al. 1999, 7. Elfström et al. 2013, 8. Grassman et al. 2005, 9. Jones et al. 2009 10. Varela and Bucher 2006, 11. Mise et al. 2016, 12. Draper et al. 2021, 13. Hazumi and Maruyama 1986, 14. Koike et al. 2011

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

**Males only

- no GUT-PASSAGE TIME was found that included fruit or seeds

+ no home range study available

APPENDIX B CHAPTER 3 SUPPLEMENTAL TABLE

Supplemental Table 1. The above models explore the effect of feeding composition and plant species on gut passage time in captive coyotes, as well as the effect of gut passage time and feeding composition on seed viability and seedling emergence (days to first emergence and total emergence) post-seed consumption and passage by a coyote. Feeding composition and gut passage time were treated as continuous variables, with the gut passage time being set at the midpoint of the relevant post-feeding interval. No covariate had a significant effect on gut passage, seed viability, or emergence. Additionally, individual variation of test subjects (coyote) accounted for a negligible amount of the residual in gut passage time.

Model formulation	Fixed Effects	Random Effects	β	S.E.	S.D.	p-value
Gut passage time ~ Feeding composition + Plant Species + (1 | Ear_Tag)	(Intercept)		14.81	0.96		<2e-16
	Feeding composition		4.02	3.92		0.31
	A. alnifolia		-0.45	2.25		0.84
	C. ehrenbergiana		-3.09	2.85		0.28
	J. osteosperma		0.02	1.87		0.99
		Individual (Ear_Tag)	3.01		1.74	
		Residual	84.95		9.22	
Viability Ratio ~ Feeding composition + Gut passage time +(1|Plant_Species)	(Intercept)		0.45	0.20		0.15
	Gut passage time		0.00	0.00		0.54
	Feeding composition		0.04	0.04		0.27
		Plant species	0.11		0.3	
		Residual	0.01		0.1	
Days to first emergence ~ Feeding composition + Gut passage time	(Intercept)		19.55	2.38		1.1e-7
	Feeding composition		-7.00	4.50		0.14
	Gut passage time		-0.01	0.17		0.95
Emergence Ratio ~ Feeding composition + Gut passage time	(Intercept)		0.15	0.11		0.17
	Feeding composition		0.35	0.20		0.10
	Gut passage time		0.00	0.01		0.71

APPENDIX C CHAPTER 4 SUPPLEMENTAL TABLES

Supplemental Table 1. The total original range of juniper (*Juniperus*), as modeled by a Maxent model of 7 juniper species. The total range colonized by juniper via either a passerine (*Passeriformes*) or coyote (*Canis latrans*) dispersal vector is reported within each time step under the year that denotes the end of that time step, as well as the total dispersal of all colonized rages that are projected to survive through 2100. Total losses account for the total amount of occupied juniper range that is projected to be lost due to climate change by 2100. All values are reported for the disperser and Shared Socioeconomic Pathways that were tested. All values are reported in km^2.

Juniper Species	Shared Social Pathway	Disperser	Original Distribution (km^2)	2021-2040 (km^2)	SE	2041-2060 (km^2)	SE	2061-2080 (km^2)	SE	2081-2100 (km^2)	SE	Total losses
J. californica	2-4.5	Passerine	1.0E+05	2.6E+04	9.3E+00	2.3E+04	2.3E+01	1.9E+04	2.9E+01	1.5E+04	2.5E+01	0.0E+00
J. deppeana	2-4.5	Passerine	8.5E+04	9.4E+03	7.4E+00	7.6E+03	1.3E+01	5.4E+03	1.2E+01	3.5E+03	1.2E+01	7.7E+02
J. monosperma	2-4.5	Passerine	2.2E+05	1.9E+04	8.8E+00	1.5E+04	2.0E+01	1.2E+04	2.2E+01	9.1E+03	2.0E+01	2.1E+02
J. Ooccidentalis	2-4.5	Passerine	1.8E+05	1.9E+04	8.9E+00	1.5E+04	1.2E+01	1.4E+04	1.3E+01	1.2E+04	1.4E+01	0.0E+00
J. osteosperma	2-4.5	Passerine	4.2E+05	8.2E+04	2.0E+01	7.0E+04	4.3E+01	5.7E+04	5.9E+01	4.5E+04	4.3E+01	0.0E+00
J. scopalorum	2-4.5	Passerine	6.3E+05	6.3E+04	1.6E+01	4.7E+04	2.9E+01	3.3E+04	2.9E+01	2.4E+04	2.5E+01	1.6E+03
J. virginiana	2-4.5	Passerine	3.6E+05	2.3E+04	1.1E+01	1.9E+04	2.4E+01	1.4E+04	2.6E+01	1.1E+04	2.7E+01	0.0E+00
Sum	2-4.5	Passerine	1.7E+06	1.4E+05	2.7E+01	1.1E+05	4.9E+01	7.9E+04	5.1E+01	6.0E+04	4.8E+01	2.6E+03
J. californica	2-4.5	Coyote	1.0E+05	7.6E+04	1.3E+01	3.8E+04	3.1E+01	3.0E+04	3.1E+01	2.6E+04	3.1E+01	0.0E+00
J. deppeana	2-4.5	Coyote	8.5E+04	3.1E+04	1.0E+01	1.2E+04	1.4E+01	6.7E+03	1.8E+01	5.2E+03	1.6E+01	7.7E+02
J. monosperma	2-4.5	Coyote	2.2E+05	7.1E+04	1.6E+01	3.4E+04	2.7E+01	2.2E+04	2.8E+01	1.7E+04	2.5E+01	2.1E+02
J. Ooccidentalis	2-4.5	Coyote	1.8E+05	7.9E+04	1.5E+01	4.1E+04	2.2E+01	2.9E+04	2.1E+01	2.3E+04	2.3E+01	0.0E+00
J. osteosperma	2-4.5	Coyote	4.2E+05	2.6E+05	2.8E+01	1.3E+05	5.1E+01	9.3E+04	5.9E+01	7.8E+04	5.5E+01	0.0E+00
J. scopalorum	2-4.5	Coyote	6.3E+05	2.3E+05	3.2E+01	1.1E+05	3.4E+01	7.5E+04	3.7E+01	5.7E+04	3.5E+01	1.6E+03
J. virginiana	2-4.5	Coyote	3.6E+05	8.1E+04	2.6E+01	5.2E+04	4.2E+01	4.2E+04	4.3E+01	4.0E+04	5.3E+01	0.0E+00
Sum	2-4.5	Coyote	1.7E+06	4.6E+05	4.5E+01	2.2E+05	5.9E+01	1.6E+05	6.2E+01	1.3E+05	7.0E+01	2.6E+03
J. californica	5-8.5	Passerine	1.0E+05	2.7E+04	9.2E+00	2.3E+04	2.5E+01	1.8E+04	2.6E+01	1.4E+04	2.7E+01	0.0E+00
J. deppeana	5-8.5	Passerine	8.5E+04	9.3E+03	7.1E+00	6.9E+03	1.4E+01	4.9E+03	1.4E+01	3.1E+03	1.1E+01	9.9E+02
J. monosperma	5-8.5	Passerine	2.2E+05	1.6E+04	8.8E+00	1.3E+04	1.8E+01	9.6E+03	2.1E+01	6.7E+03	1.7E+01	5.8E+04
J. Ooccidentalis	5-8.5	Passerine	1.8E+05	1.9E+04	8.5E+00	1.5E+04	1.2E+01	1.3E+04	1.2E+01	1.1E+04	1.2E+01	0.0E+00
J. osteosperma	5-8.5	Passerine	4.2E+05	8.2E+04	1.6E+01	6.6E+04	4.1E+01	5.3E+04	4.8E+01	3.8E+04	4.3E+01	0.0E+00
J. scopalorum	5-8.5	Passerine	6.3E+05	5.9E+04	1.5E+01	4.1E+04	2.7E+01	2.5E+04	2.5E+01	1.6E+04	1.8E+01	1.9E+04
J. virginiana	5-8.5	Passerine	3.6E+05	2.3E+04	1.2E+01	1.5E+04	2.2E+01	8.0E+03	1.8E+01	3.1E+03	1.0E+01	0.0E+00
Sum	5-8.5	Passerine	1.7E+06	1.4E+05	2.6E+01	9.7E+04	5.0E+01	6.8E+04	4.2E+01	4.6E+04	3.0E+01	7.8E+04
J. californica	5-8.5	Coyote	1.0E+05	7.7E+04	1.4E+01	3.8E+04	3.0E+01	2.9E+04	3.0E+01	2.3E+04	3.0E+01	0.0E+00
J. deppeana	5-8.5	Coyote	8.5E+04	3.0E+04	1.1E+01	1.0E+04	1.4E+01	6.4E+03	1.7E+01	5.2E+03	1.4E+01	9.9E+02
J. monosperma	5-8.5	Coyote	2.2E+05	5.0E+04	1.1E+01	2.4E+04	2.6E+01	1.7E+04	2.4E+01	1.1E+04	2.2E+01	5.8E+04
J. Ooccidentalis	5-8.5	Coyote	1.8E+05	7.9E+04	1.2E+01	4.0E+04	2.0E+01	2.8E+04	1.9E+01	2.1E+04	1.9E+01	0.0E+00
J. osteosperma	5-8.5	Coyote	4.2E+05	2.6E+05	3.6E+01	1.3E+05	5.9E+01	9.4E+04	5.5E+01	7.7E+04	4.2E+01	0.0E+00
J. scopalorum	5-8.5	Coyote	6.3E+05	2.2E+05	2.6E+01	9.9E+04	3.3E+01	6.5E+04	3.3E+01	4.8E+04	2.2E+01	1.9E+04
J. virginiana	5-8.5	Coyote	3.6E+05	7.9E+04	2.4E+01	4.3E+04	3.8E+01	3.0E+04	3.2E+01	1.9E+04	2.9E+01	0.0E+00
Sum	5-8.5	coyote	1.7E+06	4.5E+05	4.1E+01	2.0E+05	6.5E+01	1.4E+05	5.8E+01	1.0E+05	5.4E+01	7.8E+04

Supplemental Table 2. The cumulative area of juniper expansion into current grasslands at the end of each time step is modeled for dispersal by passerines (Passeriformes) and coyotes (*Canis latrans*). This table strictly accounts for areas currently defined as grasslands by the NLCD, that are predicted to be converted into juniper woodlands in future years. All values are reported for the disperser and Shared Socioeconomic Pathways that were tested. All values are reported in km^2.

Juniper Species	Shared Social Pathway	Disperser	2021-2040 (km^2)	SE	2041-2060 (km^2)	SE	2061-2080 (km^2)	SE	2081-2100 (km^2)	SE
J. californica	2-4.5	Passerine	5.1E+03	3.9E+00	9.5E+03	8.7E+00	1.3E+04	1.1E+01	1.5E+04	1.3E+01
J. deppeana	2-4.5	Passerine	1.0E+03	2.2E+00	1.9E+03	4.6E+00	2.4E+03	4.3E+00	2.6E+03	4.7E+00
J. monosperma	2-4.5	Passerine	1.8E+03	3.0E+00	3.3E+03	7.6E+00	4.6E+03	1.1E+01	5.6E+03	1.0E+01
J. Ooccidentalis	2-4.5	Passerine	2.9E+03	3.1E+00	5.5E+03	5.4E+00	8.2E+03	6.9E+00	1.1E+04	1.0E+01
J. osteosperma	2-4.5	Passerine	6.4E+03	4.4E+00	1.1E+04	1.3E+01	1.6E+04	1.9E+01	2.0E+04	2.3E+01
J. scopalorum	2-4.5	Passerine	7.4E+03	6.6E+00	1.4E+04	1.0E+01	1.9E+04	1.5E+01	2.4E+04	1.8E+01
J. virginiana	2-4.5	Passerine	1.4E+03	2.4E+00	2.4E+03	3.4E+00	3.1E+03	4.1E+00	3.7E+03	5.7E+00
Total	2-4.5	Passerine	1.8E+04	7.6E+00	3.3E+04	1.4E+01	4.5E+04	1.8E+01	5.5E+04	2.2E+01
J. californica	2-4.5	Coyote	1.3E+04	4.9E+00	1.8E+04	7.0E+00	2.1E+04	5.8E+00	2.3E+04	9.0E+00
J. deppeana	2-4.5	Coyote	4.3E+03	3.6E+00	5.8E+03	5.3E+00	7.1E+03	6.5E+00	8.2E+03	8.0E+00
J. monosperma	2-4.5	Coyote	8.8E+03	6.6E+00	1.4E+04	9.9E+00	1.7E+04	9.3E+00	1.9E+04	1.0E+01
J. Ooccidentalis	2-4.5	Coyote	1.4E+04	5.4E+00	2.2E+04	7.7E+00	2.9E+04	1.1E+01	3.4E+04	1.8E+01
J. osteosperma	2-4.5	Coyote	2.2E+04	8.9E+00	3.7E+04	2.0E+01	5.1E+04	3.0E+01	6.3E+04	3.6E+01
J. scopalorum	2-4.5	Coyote	4.5E+04	1.4E+01	7.4E+04	1.9E+01	9.6E+04	2.4E+01	1.1E+05	2.7E+01
J. virginiana	2-4.5	Coyote	7.0E+03	4.1E+00	1.2E+04	8.6E+00	1.6E+04	1.3E+01	1.9E+04	1.6E+01
Total	2-4.5	Coyote	8.2E+04	1.7E+01	1.3E+05	2.4E+01	1.6E+05	3.1E+01	1.9E+05	3.7E+01
J. californica	5-8.5	Passerine	5.4E+03	4.3E+00	9.8E+03	1.1E+01	1.3E+04	1.3E+01	1.5E+04	1.3E+01
J. deppeana	5-8.5	Passerine	1.0E+03	2.2E+00	1.7E+03	4.4E+00	2.1E+03	4.1E+00	2.3E+03	3.5E+00
J. monosperma	5-8.5	Passerine	1.4E+03	2.4E+00	2.6E+03	6.4E+00	3.8E+03	9.4E+00	4.6E+03	9.9E+00
J. Ooccidentalis	5-8.5	Passerine	2.9E+03	3.2E+00	5.6E+03	5.0E+00	8.5E+03	8.5E+00	1.1E+04	1.1E+01
J. osteosperma	5-8.5	Passerine	6.3E+03	4.9E+00	1.1E+04	1.2E+01	1.4E+04	1.5E+01	1.8E+04	1.8E+01
J. scopalorum	5-8.5	Passerine	6.9E+03	6.4E+00	1.2E+04	9.9E+00	1.6E+04	1.3E+01	1.8E+04	1.4E+01
J. virginiana	5-8.5	Passerine	1.4E+03	2.4E+00	2.1E+03	2.9E+00	2.4E+03	3.4E+00	2.5E+03	3.6E+00
Total	5-8.5	Passerine	1.8E+04	9.1E+00	3.1E+04	1.5E+01	4.1E+04	1.9E+01	4.9E+04	2.3E+01
J. californica	5-8.5	Coyote	1.4E+04	5.1E+00	1.9E+04	7.2E+00	2.1E+04	6.6E+00	2.3E+04	7.8E+00
J. deppeana	5-8.5	Coyote	4.0E+03	3.6E+00	5.2E+03	4.3E+00	6.5E+03	5.9E+00	7.7E+03	7.9E+00
J. monosperma	5-8.5	Coyote	5.3E+03	4.7E+00	8.1E+03	7.8E+00	9.5E+03	7.7E+00	1.0E+04	7.7E+00
J. Ooccidentalis	5-8.5	Coyote	1.4E+04	4.7E+00	2.2E+04	8.2E+00	2.9E+04	1.1E+01	3.4E+04	1.4E+01
J. osteosperma	5-8.5	Coyote	2.2E+04	9.7E+00	3.6E+04	2.4E+01	4.8E+04	3.0E+01	6.0E+04	3.1E+01
J. scopalorum	5-8.5	Coyote	4.3E+04	1.3E+01	6.9E+04	1.6E+01	8.6E+04	2.4E+01	9.8E+04	2.6E+01
J. virginiana	5-8.5	Coyote	6.9E+03	3.5E+00	1.1E+04	7.1E+00	1.3E+04	9.9E+00	1.4E+04	1.1E+01
Total	5-8.5	coyote	7.8E+04	1.3E+01	1.2E+05	2.2E+01	1.5E+05	2.9E+01	1.7E+05	3.4E+01

Supplemental Table 3. The estimated additional above-ground biotic carbon storage gained from juniper (*Juniperus*) encroachment into grasslands from passerines (Passeriformes) and coyote (*Canis latrans*) seed dispersal. Values are reported as the cumulative carbon added to the landscape by the end of each time step. All values are reported in Petagrams of carbon.

Juniper Species	Shared Social Pathway	Disperser	2021-2040 (Pg C)	SE	2041-2060 (Pg C)	SE	2061-2080 (Pg C)	SE	2081-2100 (Pg C)	SE
J. californica	2-4.5	Passerine	3.3E-02	7.6E-03	6.2E-02	1.4E-02	8.3E-02	1.9E-02	9.8E-02	2.2E-02
J. deppeana	2-4.5	Passerine	6.8E-03	1.5E-03	1.2E-02	2.8E-03	1.6E-02	3.6E-03	1.7E-02	3.9E-03
J. monosperma	2-4.5	Passerine	1.2E-02	2.7E-03	2.1E-02	4.9E-03	3.0E-02	6.9E-03	3.7E-02	8.4E-03
J. Ooccidentalis	2-4.5	Passerine	1.9E-02	4.3E-03	3.6E-02	8.2E-03	5.3E-02	1.2E-02	6.9E-02	1.6E-02
J. osteosperma	2-4.5	Passerine	4.2E-02	9.6E-03	7.5E-02	1.7E-02	1.0E-01	2.4E-02	1.3E-01	3.0E-02
J. scopalorum	2-4.5	Passerine	4.9E-02	1.1E-02	9.0E-02	2.0E-02	1.3E-01	2.9E-02	1.6E-01	3.6E-02
J. virginiana	2-4.5	Passerine	9.3E-03	2.1E-03	1.5E-02	3.5E-03	2.0E-02	4.6E-03	2.4E-02	5.5E-03
Total	2-4.5	Passerine	1.2E-01	2.7E-02	2.2E-01	3.5E-02	2.9E-01	3.9E-02	3.6E-01	4.2E-02
J. californica	2-4.5	Coyote	8.5E-02	1.9E-02	1.2E-01	2.6E-02	1.4E-01	3.1E-02	1.5E-01	3.4E-02
J. deppeana	2-4.5	Coyote	2.8E-02	6.4E-03	3.8E-02	8.7E-03	4.6E-02	1.1E-02	5.4E-02	1.2E-02
J. monosperma	2-4.5	Coyote	5.7E-02	1.3E-02	9.0E-02	2.1E-02	1.1E-01	2.5E-02	1.2E-01	2.8E-02
J. Ooccidentalis	2-4.5	Coyote	9.3E-02	2.1E-02	1.5E-01	3.4E-02	1.9E-01	4.3E-02	2.2E-01	5.0E-02
J. osteosperma	2-4.5	Coyote	1.4E-01	3.3E-02	2.4E-01	5.5E-02	3.3E-01	7.6E-02	4.1E-01	9.3E-02
J. scopalorum	2-4.5	Coyote	2.9E-01	6.7E-02	4.8E-01	1.1E-01	6.3E-01	1.4E-01	7.4E-01	1.7E-01
J. virginiana	2-4.5	Coyote	4.6E-02	1.0E-02	7.7E-02	1.8E-02	1.0E-01	2.4E-02	1.3E-01	2.9E-02
Total	2-4.5	Coyote	5.3E-01	1.2E-01	8.2E-01	1.4E-01	1.0E+00	1.5E-01	1.2E+00	1.5E-01
J. californica	5-8.5	Passerine	3.5E-02	8.1E-03	6.4E-02	1.5E-02	8.4E-02	1.9E-02	9.7E-02	2.2E-02
J. deppeana	5-8.5	Passerine	6.6E-03	1.5E-03	1.1E-02	2.6E-03	1.4E-02	3.1E-03	1.5E-02	3.4E-03
J. monosperma	5-8.5	Passerine	9.1E-03	2.1E-03	1.7E-02	3.9E-03	2.5E-02	5.6E-03	3.0E-02	6.9E-03
J. Ooccidentalis	5-8.5	Passerine	1.9E-02	4.3E-03	3.6E-02	8.3E-03	5.5E-02	1.3E-02	7.2E-02	1.6E-02
J. osteosperma	5-8.5	Passerine	4.1E-02	9.4E-03	7.0E-02	1.6E-02	9.4E-02	2.2E-02	1.2E-01	2.7E-02
J. scopalorum	5-8.5	Passerine	4.5E-02	1.0E-02	8.0E-02	1.8E-02	1.0E-01	2.4E-02	1.2E-01	2.7E-02
J. virginiana	5-8.5	Passerine	9.0E-03	2.1E-03	1.3E-02	3.1E-03	1.5E-02	3.5E-03	1.6E-02	3.7E-03
Total	5-8.5	Passerine	1.2E-01	2.7E-02	2.0E-01	3.3E-02	2.7E-01	3.7E-02	3.2E-01	3.8E-02
J. californica	5-8.5	Coyote	9.0E-02	2.1E-02	1.2E-01	2.8E-02	1.4E-01	3.2E-02	1.5E-01	3.4E-02
J. deppeana	5-8.5	Coyote	2.6E-02	6.0E-03	3.4E-02	7.8E-03	4.2E-02	9.7E-03	5.0E-02	1.2E-02
J. monosperma	5-8.5	Coyote	3.5E-02	7.9E-03	5.3E-02	1.2E-02	6.2E-02	1.4E-02	6.8E-02	1.5E-02
J. Ooccidentalis	5-8.5	Coyote	9.2E-02	2.1E-02	1.5E-01	3.3E-02	1.9E-01	4.3E-02	2.2E-01	5.1E-02
J. osteosperma	5-8.5	Coyote	1.4E-01	3.3E-02	2.3E-01	5.3E-02	3.1E-01	7.2E-02	3.9E-01	8.9E-02
J. scopalorum	5-8.5	Coyote	2.8E-01	6.4E-02	4.5E-01	1.0E-01	5.6E-01	1.3E-01	6.4E-01	1.5E-01
J. virginiana	5-8.5	Coyote	4.5E-02	1.0E-02	7.0E-02	1.6E-02	8.6E-02	2.0E-02	9.3E-02	2.1E-02
Total	5-8.5	coyote	5.1E-01	1.2E-01	7.7E-01	1.3E-01	9.5E-01	1.4E-01	1.1E+00	1.4E-01

CURRICULUM VITAE

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Education

PhD Utah State University, Ecology — Defense Expected December 2021
Dissertation: “Carnivore frugivory, seed dispersal and carbon storage”
Committee: Dr. Trisha Atwood (co-chair), Dr. Julie Young (co-chair), Dr. Noelle Beckman, Dr. Karin Kettenring, Dr. Ed Hammill

MS Auburn University, Wildlife Sciences — May 2017
Thesis: “Genetic diversity and connectivity of black bears (*Ursus americanus*) in Alabama”
Advisor: Dr. Todd Steury

BS University of California Davis, Wildlife, Fish, and Conservation Biology — June 2009

Research Experience

PhD Candidate, Utah State University, Logan, UT — 2018-present

Advisor: Dr. Trisha Atwood, Dr. Julie Young

- Estimated potential seed dispersal by coyotes through experimentation
- Applied projection modeling to estimate future plant distributions with different dispersal vectors
- Modeled nationwide spatial distribution of endangered species and protected areas
- Has resulted in 2 publication so far (Ecosphere, Scientific reports)

Utah State University Logan UT — 2017 to 2018
Research Associate, Dr. Julie Young

- Designed and executed experiments with captive coyotes
- Analyzed existing camera and collar datasets using multiple analytical techniques
- Resulted in 3 publications (Wildlife Society Bulletin, Animals, Human-Wildlife

Interactions)

Masters Student, Auburn University, Auburn AL 2014 to 2017
Advisor: Dr. Todd Steury

- Estimated black bear population size and genetic diversity using non-invasive techniques
- Resulted in 1 publication (PLOS)

California Department of Fish and Wildlife, CA 2011 to 2014
Scientific Aide

- Estimated black bear populations along the central coast of California utilizing non-invasive techniques
- Managed data for statewide hunting and research programs

University of Montana, MT 2011 to 2012
Backcountry Grizzly Bear Research Technician

University of Tennessee, LA 2010
Black Bear Research Technician

University of California Davis, CA 2009 to 2010
Small Mammal and Vegetation Research Technician

Grants

Utah State University Ecology Center, Research Grant ($2,500) 2019

African Safari Club of Florida, Graduate Student Scholarship ($1,500) 2017

International Association for Bear Research
& Management Conference, Travel Grant ($500) 2016

Honors and Awards

1st place graduate student poster Auburn School of Forestry
and Wildlife Sciences Spring Open House 2017

1st place graduate student poster at Southeastern 2015

Evolution and Ecology Conference

1st place graduate student poster at Alabama Chapter of The Wildlife Society Conference 2015

Publications

Journal Publications

Total citations: 59, H-index: 6

1. **Draper JP**, Atwood TB, Beckman NG, Kettenring KM, Young JK. Mesopredator frugivory has no effect on seed viability and emergence under experimental conditions. Ecosphere. 2021;12.

2. *Clancy NG, ***Draper JP**, Wolf JM, Abdulwahab UA, Pendleton MC, Brothers S, et al. Protecting endangered species in the USA requires both public and private land conservation. Scientific Reports. 2020; 10: 1–8
   **Authors contributed equally*

3. Young JK, **Draper J**, Breck S. Mind the gap: Experimental tests to improve efficacy of fladry for nonlethal management of coyotes. Wildlife Society Bulletin 2019; 43: 265–271.

4. Young, J. K., J. Golla, **J. P. Draper**, D. Broman, T. Blankenship, and R. Heilbrun. Space Use and Movement of Urban Bobcats. Animals. 2019; 9: 275.

5. Young, J. K., **J. P. Draper**, and D. Kinka. Spatial associations of livestock guardian dogs and domestic sheep. Human-Wildlife Interactions. 2019; 13: 7–15

6. **Draper, J. P**., L. P. Waits, J. R. Adams, C. L. Seals, and T. D. Steury. Genetic health and population monitoring of two small black bear (*Ursus americanus*) populations in Alabama, with a regional perspective of genetic diversity and exchange. PLoS One 2017; 12: 1–21.

7. Ordeñana, M. A., D. H. Van Vuren, and **J. P. Draper**. Habitat associations of California ground squirrels and Botta's pocket gophers on levees in California. The Journal of Wildlife Management. 2012; 76: 1712–1717.

Journal Papers in Review

1. **Draper, JP**., Rodgers, T., Young, JK., Beating the Heat: Ecology of Desert Bobcats.

Manuscript submitted for publication (BMC Ecology).

Presentations and posters

Academic

2021 ‘Coyotes as effective seed dispersers: An experimental evaluation of gut passage time and seed viability of three fruits commonly consumed by coyotes’ Ecological Society of America Annual Meeting, Virtual

2017 ‘Genetic structure of black bears (Ursus americanus) in Alabama’ Ecological Society of America Annual Meeting, Portland OR

2016 ‘Black Bear Genetic Diversity and Health in Alabama’, International Association for Bear Research & Management Annual Meeting, Anchorage AK

2016 ‘Black Bear Demographics and Genetic Health in Alabama’, Alabama State Wildlife Division Annual Meeting, Auburn AL

2015 ‘Black Bear Genetic Diversity and Health in Alabama’, Southeastern Association of Fish and Wildlife Agencies Conference, Ashville North Carolina

2015 ‘Black Bear Demographics and Habitat Use’, Alabama State Wildlife Division Annual Meeting, Auburn AL

Public

2015 ‘Alabama Black Bear Public Forum’, Heflin Alabama

2015 ‘Black Bears in Little River Canyon’, Little River Canyon National Preserve (2 Presentations)

2012 ‘Track and Sign of Wild Pigs’, California Department of Fish and Game, Advanced wild Pig Hunting Clinic, King City, CA.

Posters:

2021 ‘Carnivore Contributions to the Carbon Cycle’, The International Association for Bear Research and Management Annual Meeting, Virtual

2017 ‘Genetic diversity and connectivity of black bears (Ursus americanus) in Alabama’, Auburn School of Forestry and Wildlife Sciences Spring Open House, Auburn Alabama

2016 ‘Black Bear Genetic Diversity and Health in Alabama’, School of Forestry and Wildlife Sciences Advisory Council, Auburn Alabama

2015 ‘Black Bears in Alabama’, Governor’s One-Shot Turkey Shoot, Montgomery Alabama

2015 ‘Black Bears in Northeastern Alabama’, Alabama Chapter of the Wildlife Society Annual Meeting, Lake Guntersville Alabama

2015 ‘Black Bears in Northeastern Alabama’, Southeastern Ecology and Evolution Conference, Athens Georgia

2015 ‘Black Bears in Alabama’, School of Forestry and Wildlife Sciences Advisory Council, Auburn Alabama

Professional Training

Seminar or Workshop
Enabling Interdisciplinary and Team Science: A Professional Development Program
Presented by the American Institute of Biological Sciences, Logan, Utah, October 2-3, 2019

Professional Affiliations

Ecological Society of America
International Association for Bear Research & Management

Professional Service

Ecology Center Seminar Series Committee, Chair (2021), Member (2020)
Faculty Search Committee Student Representative (2019)
Internal Reviewer USGS (2018)
USU Graduate Student Insurance Working Group (2020)

Computer Skills

- Office Suite
- ArcGIS PRO
- Python
- R
- MARK
- Density 5.0
- Genetics software
    - Arlequin
    - FSTAT
    - GeneMapper
    - GeneMarker
    - Genalex
    - Structure
    - ML relate