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REVIEW

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REVIEW

Limitations of current knowledge about the ecology of Grey Foxes hamper conservation efforts

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Abstract: Species-specific conservation is important for maintaining the integrity of ecological communities but is dependent on sufficiently understanding multiple aspects of a species' ecology. Species-specific data are commonly lacking for species in geographic areas with little research and species perceived to have insufficient charisma or economic importance. Despite their widespread distribution across central and North America and status as a furbearing mammal, little is known about the ecology of Grey Foxes *Urocyon cinereoargenteus* compared to other species of furbearing mammals. To understand what is known about this species, especially factors affecting population dynamics, we performed a systematic review of the scientific literature. We found 234 studies about Grey Foxes, with studies increasing substantially over time but with geographic gaps in the Great Plains and most of Mexico and central America. Most studies we reviewed examined relative abundance or occupancy (n= 35), habitat associations (n= 30), primarily as part of larger mammalian community studies, or spatiotemporal effects of other mammalian carnivores (n= 19), predominately Coyote *Canis latrans*. Grey Foxes were primarily forest-associated although associations with specific forest communities or anthropogenically disturbed habitats varied among studies. Multiple studies across ecoregions reported this fox as among both the most- and least-abundant mammalian carnivore. The inter-specific effects of Coyote were often, but not exclusively, negative and were likely mediated by landscape composition and human development. Importantly, very few studies examined population-effects of coyotes on Grey Foxes. Studies of population trends, demographics, and space use of Grey Foxes were comparatively rare and small inter- and intra-study sample sizes limited our ability to infer broader patterns. We suggest multiple avenues for future research to better understand the population status of this species throughout their range.

Keywords: Abundance, co-occurrence, demography, ecology, habitat, *Urocyon cinereoargenteus*.

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Author contributions: MLA led the review of the literature and the writing of the manuscript. JMB led the statistical analyses. All authors contributed to the review of literature, statistical analyses, and writing of the manuscript.

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INTRODUCTION

Conservation biology has seen dramatic increases in effectiveness in the last century, from increasing conservation of ecological communities through bioreserves to species-specific conservation strategies. Implementation of species-specific conservation strategies has been effective at increasing species of conservation concern. For example, captive rearing and removal of lead ammunition has brought California Condors *Gymnogyps californianus* back from the brink of extinction (Walters et al. 2010), while cultural education and habitat preservation has increased populations of Giant Pandas *Ailuropoda melanoleuca* resulting in their down-listing from the endangered species list (Swaisgood et al. 2018). Species-specific conservation can be important for maintaining the integrity of ecological communities but is dependent on sufficiently understanding multiple aspects of a species' ecology. For example, modeling population viability and evaluating potential drivers of decline requires accurate estimates of demographic parameters, such as age- and sex-specific estimates of survival and fecundity (Boyce 1992; Mumme et al. 2000; Hostetler et al. 2009). Baseline estimates of abundance or occupancy are required to evaluate population trends and identify future changes in population status, while understanding habitat associations can help better assess present and future threats to population persistence (Haines et al. 2006; Aldridge et al. 2007). However, such ecological data are commonly lacking for many species, particularly those in developing countries with relatively few resources for science and conservation (Holmgren & Schnitzer 2004; Allen et al. 2020) or those perceived to have insufficient charisma or economic importance (Fuller & Cypher 2004).

Image 1 . Portrait of a Grey Fox *Urocyon cinereoargenteus* in central California.

Grey Foxes *Urocyon cinereoargenteus* are one such understudied species (Image 1). Despite their widespread distribution across Central and North America and status as a furbearing mammal (Fritzell & Haroldson 1982; Fuller & Cypher 2004), little is known about their ecology compared to other species of furbearing mammal (e.g., Sillero-Zubiri et al. 2004; Gehrt et al. 2010). Grey Foxes are currently listed as 'Least Concern' by the International Union for Conservation of Nature (Roemer et al. 2016) and do not contribute to crop damage or other sources of human-wildlife conflict (Fuller & Cypher 2004). Collectively, these factors likely work to deprioritize research and monitoring efforts for this species, especially compared to their only congener, Island Foxes *Urocyon littoralis*, which is federally endangered and a focus of large research efforts (e.g., Bakker et al. 2009). A lack of such efforts makes it difficult to detect large-scale population changes. For example, grey foxes are thought to be declining in the Midwestern USA (Bauder et al. 2020) despite minimal changes to land cover composition over the past several decades (Walk et al. 2010). However, it is unclear if such putative declines are regional in nature or more widespread. The goal of this paper, therefore, was to provide a range-wide review and synthesis of the currently available scientific literature on grey foxes to better understand their population status and ecology and identify geographic and topical gaps in the literature as avenues for future research.

Literature Review

We performed a systematic search of the scientific literature through Web of Science on 28 May 2020 using the terms ("gray fox*" OR "grey fox*" OR "Urocyon"). We then examined each entry and removed duplicate and mismatched publications (e.g., papers about island foxes), as well as those not from peer-reviewed journals or studies of captive animals. Our literature search yielded 430 peer-reviewed studies, 234 of which included research on Grey Foxes (solely or as part of a broader mammalian community). The number of studies about this species increased substantially since the 1940s (Figure 1a). Most studies were conducted within the states of California and Texas and across the southeastern

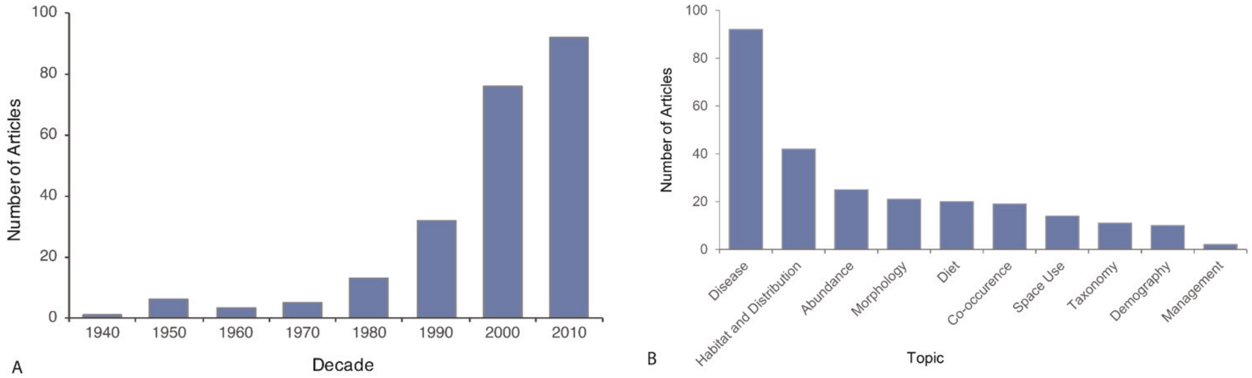


Figure 1. Number of peer-reviewed articles about Grey Foxes by decade (a) and research topic (b). An additional seven articles published in 2020 were used in our review but not included in this figure.

USA (Figure 2). Major gaps in the geographic distribution of studies about Grey Foxes included the Great Plains ecoregion in the midwestern United States and wet and dry tropical forests ecoregions across Mexico and central America (Figure 2). We further describe the geographic distribution of studies with reference to the Level I Ecological Regions of North America (Omernik & Griffith 2014; Appendix 1).

We classified the 234 studies of grey foxes into ten topical categories (Figure 1b). Most studies focused on disease (n= 92 articles) followed by habitat and distribution (n= 42 articles). All other categories had < 25 studies (Figure 1b). We focused our review on five categories we deemed most relevant to the management and conservation of these foxes defined as follows: 1) Abundance: spatiotemporal estimates of the absolute or relative number of individuals, density, or occupancy; 2) Demography: estimates of population vital rates (e.g., survival rates, mortality rates, sex ratio, mean age, litter size); 3) Habitat: modeling aspects of ecology or behavior of Grey Foxes (e.g., spatial locations, home range size, occupancy, or relative abundance) as a function of one or more habitat features (e.g., vegetation characteristics, land cover type, etc.); 4) Co-occurrence with dominant carnivores: evaluated the spatiotemporal distribution or interactions of Grey Foxes in relation to other carnivores; and 5) Space Use: spatial distribution of individual Grey Fox. We separated distribution studies from habitat studies for further consideration because the former dealt exclusively with distributional or range expansion records. We also included studies reporting occupancy estimates in abundance rather than distribution because such studies occurred across relatively limited geographic extents. We only included demography studies that reported model-based estimates of vital rates. Similarly, we excluded habitat studies that were purely descriptive and lacking an underlying statistical model. For co-occurrence with dominant carnivores, we only considered studies that statistically examined how mammalian carnivores directly affected these foxes through statistical analyses.

We found seven distribution studies (Figure 2). Three studies provided records extending the distribution of Grey Foxes in New Brunswick (Mcalpine et al. 2008), Alberta (Moore 1952), and South Dakota (Schantz 1950). Two studies also reported new within-range occurrence records in New Mexico (Anderson & Stuart 1993) and Texas (Jones & Frey 2008), USA. Peterson (1953) described the historical and contemporary distribution of this species in Ontario, and Zielinski et al. (2011) found that the distribution of these foxes in the Sierra Nevada was similar between the early 1900s and 1996–2002, but Grey Foxes were detected less frequently during 1996–2002.

Abundance

We found 25 studies that reported abundance of Grey Foxes and 10 studies reporting occupancy. All but three of the studies reported these foxes as part of the larger mammalian or carnivore community. Most studies that reported relative abundance (RAB) for this species used camera traps (n= 14), track and scat transects (n= 6), or track plots (n= 3). Hair snares (Downey et al. 2007), observations by archery deer hunters (Cooper et al. 2012), and environmental DNA (eDNA, Klymus et al. 2017) were each reported detecting Grey Foxes by a single study.

Distributions of RAB estimates from camera trap and transect studies were generally similar across ecoregions (Figure 3). Studies with relatively high RAB occurred in multiple ecoregions including the Temperate Sierras (Cunningham et al. 2006; Gallina et al. 2016), Eastern

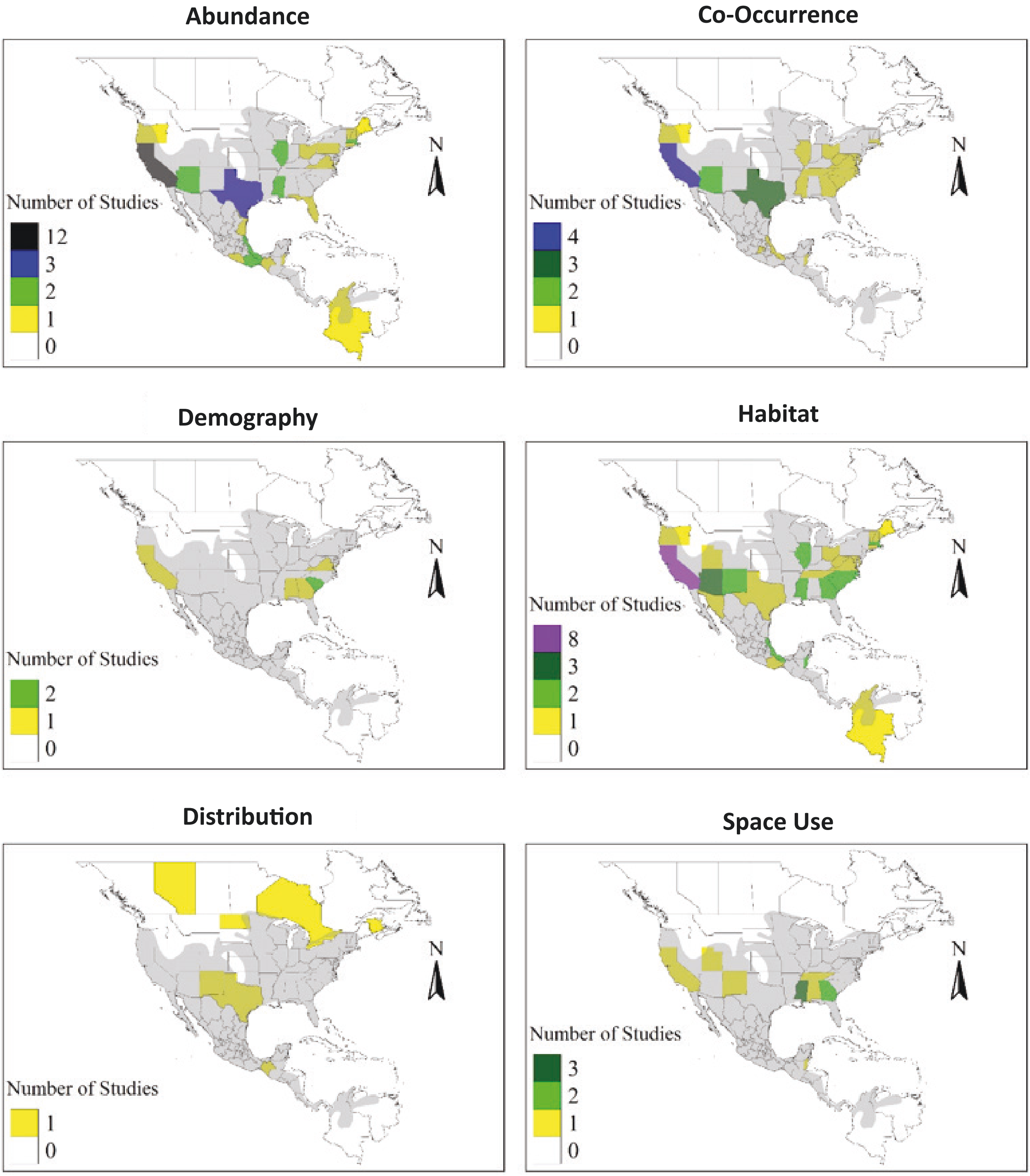


Figure 2. Geographic distribution of published peer-reviewed studies of Grey Fox ecology by category considered in this literature review. Grey shaded areas represent the contemporary distribution of Grey Foxes from the International Union for Conservation of Nature Red List (Roemer et al. 2016). Note that a single abundance, co-occurrence, and space use study were conducted in Belize.

Temperate Forests (Chamberlain et al. 1999), Tropical Wet Forests (Davis et al. 2011), Mediterranean California (Allen et al. 2017), Great Plains (Karlin & De La Paz 2015), and Marine West Coast Forests (Eriksson et al. 2019). To further explore geographic variation in abundance of Grey Foxes, we calculated the rank-order of RAB or occupancy across all mammalian carnivores detected in the study, including grey fox. We then calculated the number of studies where these foxes were in the top, middle, or bottom third ranks across seven ecoregions. Grey Foxes were among the most abundant carnivores in Mediterranean California, Northwestern Forested

Mountains, and Tropical Dry Forests ecoregions and among the least abundance carnivores in the Eastern Temperate Forests and Tropical Wet Forests ecoregions (Figure 4). This species ranked among the top third in at least one study within each ecoregion and in the bottom third in at least one study in five ecoregions. Our results indicate that Grey Foxes may show substantial intra- and inter-regional variation in abundance and highlight the value of mammalian community studies for obtaining information on their abundance and distribution.

Relatively few studies reported trends in RAB of Grey Foxes and these studies were limited in geographical scope. Long-term studies in Pennsylvania using bounty records (Richmond 1952) and in Texas using nocturnal spotlight surveys (Schwertner et al. 2006) reported positive trends over 15 and 25 years, respectively. A 15-year study in Mississippi using trapper harvest records reported stable trends (Lovell et al. 1998). Other studies evaluating temporal variation in RAB or occupancy of this species were conducted over relatively short (<3 year) periods (Chamberlain et al. 1999; Cunningham et al. 2006; Gallina et al. 2016). In contrast, Bauder et al. (2020) found evidence of declines in Grey Foxes in Illinois over 43 years and two studies in the midwestern USA found that they were the least prevalent species in the native carnivore community (Lesmeister et al. 2015; Rich et al. 2018). Lesmeister et al (2015) found that site extinction rates for these foxes were higher than site colonization rates, and other studies have suggested declines of Grey Foxes in the midwestern USA (Cooper et al. 2012). Our literature review suggests that this species can exhibit relatively high abundance in many parts of their range, but the paucity of long-term studies about these foxes make it difficult to evaluate their range-wide population status. Future Grey Fox monitoring efforts should consider the diverse factors necessary for optimizing statistical power to detect trends over a specified monitoring period, including initial abundance, sampling method, number of sites, study length, and state variable (e.g., occupancy or RAB; Maxwell & Jennings 2005; Mahard et al. 2016; Brown et al. 2017; Ward et al. 2017).

Demography

Six studies reported demographic parameter estimates and all but one was from the Eastern Temperate Forest with the sixth from Mediterranean California (Figure 2). Three studies reported mean annual survival rates of 0.58–0.69 (Table 1). Studies did not report statistically significant differences in survival between adults and juveniles or males and females (Chamberlain & Leopold 2000; Farias et al. 2005; Temple et al. 2010) although one study found that adult annual survival (0.77) was nearly twice that of juveniles (0.34; Farias et al. 2005). Reported sources of mortality for Grey Foxes included legal harvest, predation, vehicle mortality, canine distemper, canine hepatitis, and rabies (Chamberlain & Leopold 2000; Weston & Brisbin 2003; Farias et al. 2005; Glenn et al. 2009; Temple et al. 2010). Model-based estimates of annual cause-specific mortality included 0.34 for human-caused (Temple et al. 2010) and 0.42 for predator-caused (Farias et al. 2005) mortality. Coyotes *Canis latrans* were the primary cause of predation mortality (Weston & Brisbin 2003; Farias et al. 2005) although predation by Bobcats *Lynx rufus* was also reported (Farias et al. 2005). The percentage of confirmed mortalities from Coyote predation varied from 28.6% (Weston & Brisbin 2003) to 67% (Farias et al. 2005).

Estimates of other demographic parameters were only available from a single population in South Carolina, with a mean population age of 3.5 years and a slightly female-biased sex ratio (31:44; Weston & Brisbin 2003). Estimated fecundity from corpora lutea counts was 1.94–

Table 1. Survival estimates for Grey Foxes (estimates are pooled across sexes and seasons unless otherwise noted).

Study	Location	Sample size	Time period	Estimation method	Survival (95% CI)	Legal harvest
Farias et al. 2005	California	17 7 15 7 n/a n/a	Annual Adult Annual Adult Female Annual Adult Male 8-month Juvenile 8-month Juvenile Female 8-month Juvenile Male	MICROMORT	0.58 (0.39–0.85) 0.69 (0.41–1.00) 0.49 (0.27–0.88) 0.34 (0.11-0.99) 0.40 (0.11–1.00 0.30 (0.06–1.00)	No
Temple et al. 2010	Georgia	33	Annual 4-month (Breeding) 4-month (Kit-rearing) 4-month (Winter)	Kaplan-Meier	0.61 (0.41–0.81) 0.81 (0.68–0.95) 0.75 (0.55–0.94) 0.82 (0.64–0.99)	Yes
Chamberlain & Leopold 2000	Mississippi	37	Annual	Not reported*	0.56	Yes
Weston & Brisbin 2003	South Carolina	75	Annual	Krebs (1999)	0.69 (0.63–0.74)	No

* Estimated reported in Farias et al. (2005) based on calculations from data in Chamberlain & Leopold (2000).

Table 2. Summary of habitat associations of Grey Foxes, with the direction of effect presented as negative (-), positive (+), or no effect. Studies were classified as no effect when a given habitat feature was used in proportion to availability, coefficient estimates were not reported (e.g., covariate removed via step-wise model selection), or if the habitat was not the most significantly used habitat within a compositional analysis. Asterisks indicate strong empirical support and multiple symbols per study or habitat indicate multiple sampling methods or spatial scales. Habitats include forest (FRST), hardwood forest (HARD), coniferous forest (CONF), chaparral or shrub (SHRB), habitat heterogeneity (e.g., heterogeneity in landscape composition, habitat edge; HTRO), agriculture (AGRI), and anthropogenic (e.g., urban, roads; ANTH).

Citation	Location	FRST	HARD	CONF	SHRB	HTRO	AGRI	ANTH
Barrett et al. 2012	Arizona	–						
Cunningham et al. 2006	Arizona	+/–						
Reed 2011	Arizona	.						
Davis et al. 2011	Belize	–						
Harmsen et al. 2019	Belize	./+/–					.	
Borchert 2012	California	–*						
Farias et al. 2012	California		.		+*			–*
Kowalski et al. 2015	California							–*
Markovchick-Nicholls et al. 2008	California							–*
Ordenana et al. 2010	California		+*		.			–*
Patten & Burger 2018	California							–*
Schuette et al. 2014	California	+						.
Pineda-Guerrero et al. 2015	Colombia	+*					–*	
Deuel et al. 2017	Georgia		+*	+	+/+*	+	+/+*	+*
Temple et al. 2010	Georgia		+/+*	+/+*	–*/+*		–/+*	+*
Cooper et al. 2012	Illinois	+				+	–	
Lesmeister et al. 2015	Illinois	+*				+*	–*	+*/–*
LeFlore et al. 2019	Massachusetts	.					–	.
Gallina et al. 2016	Mexico	–*					+*	+*
Perez-Solano et al. 2018	Mexico	+*					–	
Rota et al. 2016	Mid-Atlantic States							./+*
Chamberlain et al. 2000	Mississippi		./+*	./+*				
Constible et al. 2006	Mississippi					–/+		
Pearman-Gillman et al. 2020	New England		.	.	.	+*	+*	.
Harrison 1993	New Mexico	+*						
Harrison 1997	New Mexico	+*/–*						+*/–*
Rich et al. 2018	Ohio	–			–		–/+	–
Eriksson et al. 2019	Oregon				+*			
Sawyer & Fendly 1994	South Carolina		./–	+*/–*				
Lombardi et al. 2017	Texas							./–*

3.6 pups/litter (Weston & Brisbin 2003), and mean litter size was 3.1 (n= 8 litters, range= 2–5; Glenn et al. 2009).

The paucity of demographic studies on Grey Foxes and their limited sample sizes and geographic scope represent a substantial gap in our understanding of their population ecology. Accurate demographic parameter estimates, particularly sex- and age-specific survival and fecundity estimates, are important for evaluating population viability and understanding causes of temporal changes in population size. We therefore encourage future studies across the species range to provide model-based demographic parameter estimates. The potential for high Coyote mortality may have important implications for population dynamics of Grey Foxes as Coyotes have expanded their distribution across North and central America (Gompper 2002; Hody & Kays 2018).

Table 3. Summary of effects of larger carnivores on spatial overlap with Grey Fox, with the direction of effect presented as negative (-), positive (+), or no effect. Studies were classified as no effect when the inter-specific effect was not reported or if predicted occupancy values were ≤0.02 between sites with and without the other carnivore (Lesmeister et al. 2015). Asterisks (*) indicate strong empirical support (*P* value < α, 95% CI excluded zero, model with inter-specific effect has greater AIC weight than an intercept- or habitat-only model, species interaction factor > 1.5 or < 0.5). Studies with multiple directions of effect refer to multiple sampling scales. Rota et al. (2016) encompassed the states of Maryland, Virginia, West Virginia, Tennessee, North Carolina, and South Carolina.

Study	Location	Bobcat (*Lynx rufus*)	Coyote (*Canis latrans*)	Fisher (*Pekania pennant*)	Jaguar (*Panthera onca*)	Ocelot (*Leopardus pardalis*)	Puma (*Puma concolor*)	Raccoon (*Procyon lotor*)	Red Fox (*Vulpes vulpes*)
Atwood et al. 2011	Texas	–*	–*						
Barrett et al. 2012	Arizona		–*					+*	
Borchert 2012	California		.						
Chamberlain & Leopold 2005	Mississippi	–	–						
Davis et al. 2011	Belize				–	–	+		
Fedriani et al. 2000	California		–*						
Green et al. 2018	California/Oregon			–*					
LeFlore et al. 2019	Massachusetts		–					–	.
Lesmeister et al. 2015	Illinois	.	./–*						+*
Lombardi et al. 2017	Texas		.						
Reed 2011	Arizona	–	–*						
Rich et al. 2018	Ohio	–	+					–	–
Rota et al. 2016	Mid-Atlantic States	–	+						+*

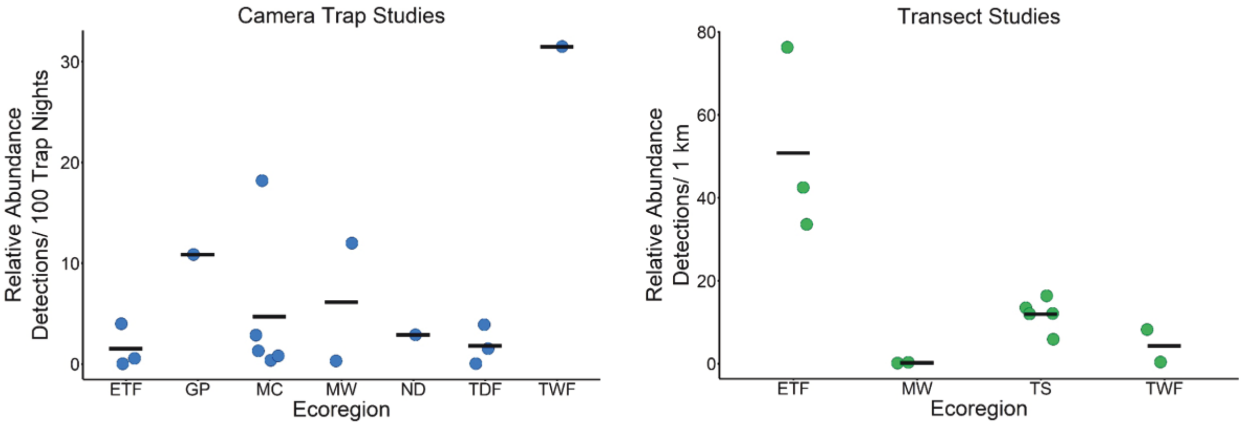


Figure 3. Relative abundance of Grey Foxes across Level I ecoregions (Omernik & Griffith 2014) from studies using camera traps (detections/100 trap nights, A) or line transect surveys (detections/1 km, B). Horizontal bars represent mean values. Ecoregions are: ETF= Eastern temperate forest, GP= Great plains, MC= Mediterranean California, MW= Marine West Coast Forest, ND= North American Desert, TDF= Tropical Dry Forest, TWF= Tropical Wet Forest, TS= Temperate Sierras.

However, our review illustrates that Coyote predation on Grey Foxes can vary widely across populations and future studies could focus on linking individual-level effects of predation from Coyotes to population-level responses of Grey Foxes.

Habitat

We found 30 studies that modeled habitat associations of Grey Foxes (Table 2) excluding an additional four studies that were purely descriptive and therefore were not included in subsequent totals. Most habitat studies used camera traps (n= 14), either in isolation or with other sampling methods, followed by transect sampling (tracks or scat; n= 8), very high frequency (VHF) (n= 6) or global positioning system telemetry (n= 1), and observations by archery deer hunters (n= 1). Studies occurred in a diverse range of landscape types including urban, natural areas surrounded or adjacent to urban areas, pinyon-juniper forest, chaparral, eastern deciduous & coniferous forest, and tropical forest (Table 2). Studies were conducted in East Temperate Forest, Mediterranean California, Temperate Sierras, and Tropical Dry Forest ecoregions (Figure 4).

Grey Foxes were positively associated with forest environments throughout their range, although associations with other vegetation communities or structural features varied geographically (Table 2). For example, Grey Foxes in California and Oregon were often positively associated with chaparral or shrub-scrub habitats (Fedriani et al. 2000; Farias et al. 2012; Erikson et al. 2019). Several studies found weak or no association with forest-related covariates including forest cover (Rich et al. 2018), canopy cover (Davis et al. 2011; Reed 2011), distance to nearest forest (LeFlore et al. 2019), or basal area (Barrett et al. 2012) perhaps reflecting insufficient covariate variability within the study area or regional variation in habitat associations. Results from several studies suggest that these foxes may use more open forest environments (Barrett et al. 2012; Borchert 2012), edge habitats (Davis et al. 2011; Deuel et al. 2017; Harmsen et al. 2019; Pearman-Gillman et al. 2020), and heterogenous landscapes (Cooper et al. 2012; Lesmeister et al. 2015; but see Constible et al. 2006). Despite the methodological variation across studies, our review highlights the importance of forest environments for Grey Foxes across their range.

Early research indicated that Grey Foxes were closely associated with hardwood forest (Fritzell & Haroldson 1982). Studies in pine-dominated landscapes within the Eastern Temperate Forest ecoregion reported selection for hardwood forest although the degree of selection varied by spatial scale and season (Sawyer & Fendly 1994; Chamberlain et al. 2000; Temple et al. 2010; Deuel et al. 2017). Selection for mature (≥ 30-year) and 9–15-year-old pine and mixed pine-hardwood forests was also reported (Chamberlain et al. 2000). Hardwood species may offer vertical escape cover from Coyotes given the climbing abilities of Grey Foxes (Fritzell & Haroldson 1982) and small mammal prey may also be more abundant in hardwood forests (Chamberlain et al. 2000; Temple et al. 2010; Lesmeister et al. 2015). However, few studies in landscapes not dominated by coniferous forests directly compared selection of hardwood and coniferous forest (Table 2). Ordenana et al. (2010) reported positive associations with oak woodland in California but Lesmeister et al. (2015) reported an overall negative association between Grey Foxes and hardwood forests in forest-agriculture landscapes in southern Illinois. However, Lesmeister et al. (2015) found that these foxes were more likely to use hardwood forests when Coyotes were present. Our review suggests that associations of this species with hardwood forest may not be universal but rather conditional upon the broader landscape context and carnivore community. We encourage future research evaluating the role of vegetation community, structural characteristics (e.g., canopy cover), resource availability (e.g., small mammal abundance), and carnivore community on habitat suitability for Grey Foxes.

Studies evaluating associations of Grey Foxes with anthropogenic development (e.g., urbanization, roads) often reported conflicting information (Table 2). Several studies reported negative associations between Grey Foxes and anthropogenic development (e.g., Markovchick-Nicholls et al. 2008; Ordennana et al. 2010; Farias et al. 2012; Kowalski et al. 2012; Lombardi et al. 2017), yet other studies found that these foxes utilize a range of human development intensities (Harrison 1993, 1997; Riley 2006; Kapfer & Kirk 2012; Lombardi et al. 2017). Similarly, associations of Grey Foxes with agriculture varied among studies. For example, studies from forest-agriculture landscapes in the Eastern Temperate Forest ecoregion reported negative associations with agriculture (Cooper et al. 2012; Lesmeister et al. 2015) as well as positive or neutral associations (Temple et al. 2010; Deuel et al. 2017; Pearman-Gillman et al. 2020). The particular response of Grey Foxes to anthropogenic land covers may depend on factors including the intensity of human or agricultural development, resource availability, diel period, or the local carnivore community (Harrison 1997; Rota et al. 2016; Nickel et al. 2020). For example, positive association of these foxes with anthropogenic development may reflect avoidance behavior of Coyotes (Lesmeister et al. 2015; Wang et al. 2015) and agricultural edges may offer food from crops and small mammal prey (Temple et al. 2010; Cortes-Marcial et al. 2014). The impacts of anthropogenic landscape change on the habitat associations of this species therefore represents an important avenue of future research to better understand population dynamics of Grey Foxes.

Co-occurrence with Dominant Carnivores

We reviewed 19 studies that evaluated interactions between Grey Foxes and other carnivores by analyzing spatial (n= 13) or temporal overlap (n= 5) or by reporting predation events (n= 4). These studies most frequently used camera traps (n= 14), and to a lesser degree track plates (n= 3), scat collection (n= 3), radio-telemetry (n= 2), and spotlight surveys (n= 1). Studies were conducted in East Temperate Forest, Mediterranean

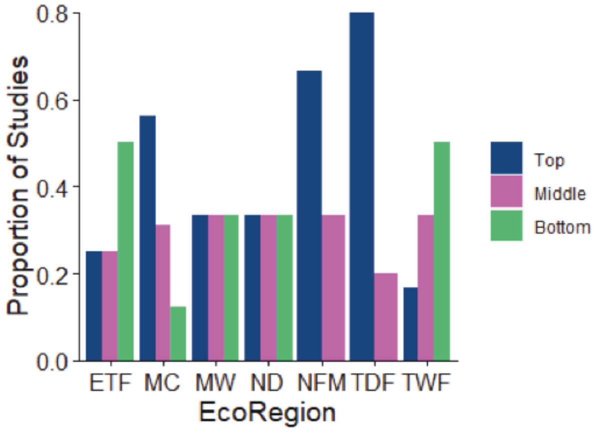


Figure 4. Proportion of studies where the rank order of abundance or occupancy of Grey Foxes was in the top, middle, or bottom third across all mammalian carnivores Results are presented by Level I ecoregion (Omernik & Griffith 2014): ETF= Eastern Temperate Forest, MC= Mediterranean California, MW=Marine West Coast Forest, ND= North American Desert, NFM= Northwestern Forested Mountains, TDF= Tropical Dry, Forest TWF= Tropical Wet Forest. Three ecoregions (Great Plains, Northern Forests, Temperate Sierras) were excluded due to only one study occurring there.

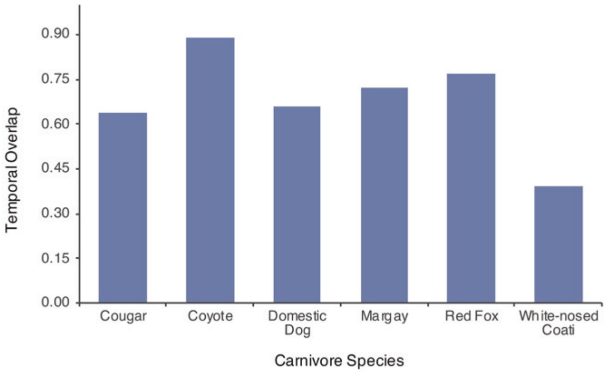


Figure 5. Estimates of temporal overlap between Grey Foxes and co-occurring mammalian carnivores (Gomez-Ortiz et al. 2019; LeFlore et al. 2019; Mella-Mendez et al. 2019). Overlap values range from zero (no overlap) to one (complete overlap).

California, Maritime West Coast Forest, Northwestern Forested Mountains, North American Deserts, Great Plains, Temperate Sierras, and Tropical Dry Forest (Figure 4).

Most studies (n= 7 of 11) that examined spatiotemporal interactions between Grey Foxes and Coyotes found evidence of negative effects of Coyotes on these foxes (Table 3), consistent with the general expectation that Coyote negatively affect smaller sympatric canids (Donadio & Buskirk 2006). In a rare experimental study, Henke & Bryant (1999) found that RAB of Grey Foxes in western Texas increased following removal of Coyotes. However, negative effects of Coyotes were often weak or not statistically significant (Borchert 2012; Lombardi et al. 2017; LeFlore et al. 2019) and two studies reported positive effects (Rota et al. 2016; Rich et al. 2018). Showing similar contrasts, LeFlore et al. (2019) reported near complete temporal overlap between Coyotes and Grey Foxes (Figure 5) while Lesmeister et al. (2015) found that these foxes were detected less frequently during nights when Coyotes were also detected. Such variability may be at least partially explained by variation in sampling unit spatial scale and landscape conditions (Lesmeister et al. 2015). For example, Chamberlain & Leopold (2005) found extensive home range overlap between Coyotes and Grey Foxes but very little core area overlap. Similarly, Rota et al. (2016) found that occupancy of this species in the presence of Coyotes increased with increasing human development although Lombardi et al. (2017) found no spatial relationships between these foxes and Coyotes within urban landscapes. We therefore encourage studies evaluating interactions within carnivore communities to consider the potential effects of scale and landscape context in their analyses.

Relatively few studies reported interactions of Grey Foxes with other carnivores (Table 3). Five of six studies including Bobcats reported negative effects on these foxes but the strength of these relationships was often low (Table 3). Interestingly, two of four studies reported strong positive relationships between occupancy of Grey Foxes and Red Foxes (Lesmeister et al. 2015; Rota et al. 2016). Davis et al. (2011) examined relationships between the RAB of Grey Foxes and three larger sympatric felids but low empirical support for inter-specific effects. However, other studies have shown that larger carnivores (i.e., Puma *Puma concolor*) can have a positive effect on Grey Foxes by directly limiting Coyotes (Allen et al. 2015, 2017). Other species may also have positive effects on Grey Foxes and more research is needed to understand the interactive relationships between Grey Foxes and the larger mammalian carnivore community.

Space Use

We found 11 studies that reported space use estimates for Grey Foxes. Ten studies used VHF telemetry and one used global positioning system (GPS) telemetry. Multiple home range estimation methods were used within and across studies including minimum convex polygons and fixed or adaptive kernel estimators (Table 4). All but three studies were conducted in the Eastern Temperate Forest (Figure 2).

Estimated home range sizes for Grey Foxes varied by almost an order of magnitude across studies (range= 0.69–6.69 km^2, Table 4). However, variation in home

Table 4. Home range (100 % and 95 %) and core area (50 %) sizes (km^2 and standard errors in parentheses) estimates for Grey Foxes and the number of individuals used for each estimate (n). Estimation methods include minimum convex polygons (MCP), adaptive kernel (AK), or fixed kernel (FK) estimators.

Reference	HR calculation method	Composite HR	Breeding HR	Pup-rearing HR	Non-breeding HR
Harrison 2002	95 % MCP	4.81 (1.79)			
Greenberg et al. 1994	100 % MCP	3.97 (1.51)	2.72 (0.17)^{a}	2.32 (0.43)^{b}	2.83 (0.42)^{c}
Trapp 1978	100 % MCP	1.07			
Riley et al. 2006	95 % MCP	0.69 (0.03)°			
Chamberlain & Leopold 2000	95 % AK		3.53 (0.20)^{d}	2.02 (0.20)^{e}	1.66 (0.19)^{f}
Temple et al. 2010	95 % FK		0.91 (0.13)^{d}	1.00 (0.18)^{e}	1.52 (0.32)f
Harmsen et al. 2019	95 % Kernel area*	3.31-6.69			
	HR calculation method	Winter HR (Jan–March)	Spring HR (April–June)	Summer HR (July–Sept)	Fall HR (Oct–Dec)
Deuel et al. 2017	95 % FK	2.17 (0.54)	1.61 (0.32)	2.15 (0.32)	2.01 (0.43)
	HR calculation method	Gender	Pre-mate loss HR	Post-mate loss HR	Percent Change
Chamberlain et al. 2002	95 % FK	Female	4.48	6.37	30%
		Male	2.86	17.16	83%
		Male	2.19	0.93	-58%
		Female	0.96	0.64	-33%

range estimation method and tracking duration limited our ability to determine the extent to which this variation was methodological or due to seasonal, regional, or environmental variation. For example, Chamberlain et al. (2000) and Temple et al. (2010) found that home range sizes of Grey Foxes varied seasonally but Greenberg et al. (1994) and Deuel et al. (2017) found that home range sizes were similar across seasons. Several studies reported that home range sizes were similar between sexes and among age classes (Greenberg et al. 1994; Chamberlain & Leopold 2000; Riley 2006; Temple et al. 2010; Deuel et al. 2017). Lack of inter-sexual differences in home range size may reflect the widespread presence of pair-bonding in Grey Foxes (Greenberg et al. 1994; Chamberlain et al. 2000; Riley 2006; Deuel et al. 2017). In contrast to studies of other canids (e.g., Riley et al. 2003; O'Donnell & delBarco-Trillo 2020), studies of Grey Foxes in and near urban environments found that home range size was not strongly affected by urban development (Harrison 1997; Riley 2006). The limited number and geographic distribution of studies of space use by these foxes, combined with high methodological variability, inhibit our ability to infer general patterns of space use by this species. We therefore encourage additional studies of the spatial ecology of Grey Foxes and recommend that researchers standardize tracking duration and home range estimation methods across studies to facilitate inter-study comparisons.

The degree of home range overlap varied within and between sexes. Several studies reported that intra-sex home range overlap and overlap between unbonded males and females was relatively low while home range overlap between bonded adult male-female pairs relatively high (Greenberg et al. 1994; Chamberlain et al. 2000; Riley 2006; Deuel et al. 2017). However, Deuel et al. (2017) found multiple instances of extra-home range forays in both males and females which may reflect attempted extra-pair copulations (e.g., Glenn et al. 2008). Home range overlap between adults and subadults was also relatively high (Greenberg et al. 1994). It is likely that instances of low home range overlap are explained by territoriality while high spatial overlap between bonded pairs likely reflects shared duties of pup-rearing (Nicholson et al. 1985; Chamberlain & Leopold 2000, 2002; Elbroch & Allen 2013). However, the mechanisms for maintaining or defending territorial boundaries appear to be largely unexplored in Grey Foxes. Because patterns of spatial overlap are important in ultimately influencing population density and carrying capacity, future research could focus on describing the degree of and environmental factors influencing home range overlap for Grey Foxes.

CONCLUSIONS

Our review provides a summary of the ecology of Grey Foxes for researchers and managers, while also highlighting several existing gaps in our knowledge. We found large gaps in geographic distribution of published studies about Grey Foxes, as most studies were conducted in the southeastern or southwestern USA. In contrast, Mexico, central America, and more northerly latitudes of their range were underrepresented in our review. A paucity of demographic and space use studies was particularly striking and limits our understanding of how individual-level effects of landscape features and sympatric carnivores may affect population-level processes of Grey Foxes. Additional demographic and space use studies of Grey Foxes in anthropogenically developed landscapes within the context of the larger carnivore community could help better understand the extent to which populations of these foxes in those landscapes are self-sustaining or acting as population sinks.

While Grey Foxes can be locally abundant throughout their range, long-term data on the RAB or occupancy of these foxes is scarce and often limited to harvest records which are subject to a range of potentially confounding factors (e.g., trapper effort and pelt prices; Bauder et al. 2020). We were therefore unable to assess the population status of Grey Foxes throughout much of their range although our results largely support the hypothesized decline of these foxes in the midwestern USA. However, the mechanisms for such a decline are unclear. While our review provides evidence that Coyote can negatively affect the behavior and survival of grey foxes, the magnitude of such effects can vary and may depend on study-specific conditions such as habitat availability or resource abundance. However, the effects of competing canids are complex because of range-wide shifts, including the recent expansion of coyotes into eastern North America (Gompper 2002; Hody & Kays 2018). These changes in canid and carnivore distributions shift dynamics in communities, but they also make the lack of information on Grey Foxes more important because we do not have historical baseline data to help us interpret current Grey Fox distribution, abundance, and ecology.

We offer several suggestions for avenues of future research on Grey Foxes. First, we recommend additional demographic studies on Grey Foxes to allow for more rigorous estimates of population viability and trends. Second, we encourage researchers to examine existing data sets from mammalian carnivore community studies and furbearer harvest records to provide additional information on geographic variation of population trends in Grey Foxes. While researchers must account for temporal variation in trapper or hunter harvest effort (e.g., Bauder et al. 2020), harvest data are regularly recorded by wildlife management agencies and may represent the longest, most spatially diverse data set available for evaluating the population trends of Grey Foxes. Third, a systematic review of the effects of disease on population ecology of Grey Foxes by experts in the field would be beneficial. Finally, we encourage additional research on interactions between Grey Foxes and Coyotes to evaluate the extents to which Coyotes influence the population dynamics of these foxes. Finally, citizen science has been used to inform the ecology and management of other canids (Mueller et al. 2019) and could be a beneficial approach for future studies.

As with many studies, we encourage researchers to use analytical approaches that allow for the standardized reporting of estimates to facilitate future comparisons across studies. Methodological variation among studies we reviewed made inter-study comparisons difficult which compounded the problem of low numbers of studies. For example, our ability to compare estimates of home range sizes of Grey Foxes were greatly hindered by variation in sampling method, estimation technique, and temporal period length. Similarly, studies of habitat associations of Grey Foxes varied widely in their environmental covariates and analytical approaches which also hindered inter-study comparisons. We also encourage researchers to deposit data in open-access repositories (e.g., movebank or dryad) to facilitate future comparisons between studies.

REFERENCES

Allen, M.L., L.M. Elbroch, C.C. Wilmers & H.U. Wittmer (2015). The comparative effects of large carnivores on the acquisition of carrion by scavengers. *American Naturalist* 185(6): 822–833. https://doi.org/10.1086/681004

Allen, M.L., M.S. Gunther & C.C. Wilmers (2017). The scent of your enemy is my friend? The acquisition of large carnivore scent by a smaller carnivore. *Journal of Ethology* 35(1): 13–19. https://doi.org/10.1007/s10164-016-0492-6

Allen, M.L., A. Inagaki & M.W. Ward (2020). Cannibalism in raptors: a review. *Journal of Raptor Research* 54(4): 424-430. https://doi.org/10.3356/0892-1016-54.4.424

Anderson, R.E. & J.N. Stuart (1993). The gray fox, *Urocyon cinereoargenteus*, on the Llano Estacado of New Mexico. *The Texas Journal of Science* 45(4): 354–355.

Atwood, T.C., T.L. Fry & B.R. Leland (2011). Partitioning of anthropogenic watering sites by desert carnivores. *Journal of Wildlife Management* 75(7): 1609–1615. https://doi.org/10.1002/jwmg.225

Bakker, V.J., D.F. Doak, G.W. Roemer, D.K. Garcelon, T.J. Coonan, S.A. Morrison, C. Lynch, K. Ralls & R. Shaw (2009). Incorporating ecological drivers and uncertainty into a demographic population viability analysis for the island fox. *Ecological Monographs* 79(1): 77–108. https://doi.org/10.1890/07-0817.1

Barrett, K.J., E.L. Kalies & C.L. Chambers (2012). Predator occupancy rates in a thinned ponderosa pine forest, Arizona: a pilot study.

Wildlife Society Bulletin 36(2): 232–239. https://doi.org/10.1002/wsb.124

Bauder, J.M., M.L. Allen, A.A. Ahlers, T.J. Benson, C.A. Miller & K.W. Stodola (2020). Identifying and controlling for variation in canid trapper harvest data. *Journal of Wildlife Management* 84(7): 1234–1245. https://doi.org/10.1002/jwmg.21919

Brown, D.J., M.M. Cochrane & R.A. Moen (2017). Survey and analysis design for wood turtle population monitoring. *Journal of Wildlife Management* 81(5): 868–877. https://doi.org/10.1002/jwmg.21249

Borchert, M.I. (2012). Mammalian carnivore use of a high-severity burn in conifer forests in the San Bernardino mountains of Southern California, USA. *Hystrix-Italian Journal of Mammalogy* 23(2): 50–56. https://doi.org/10.4404/hystrix-23.2-5610

Boyce, M.S. (1992). Population viability analysis. *Annual Review of Ecology and Systematics* 23(1): 481–506.

Chamberlain, M.J., J.W. Mangrum, B.D. Leopold & E.P. Hill (1999). A comparison of attractants used for carnivore track surveys. *Proceedings of the Fifty-Third Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 53(1): 296–304.

Chamberlain, M.J. & B.D. Leopold (2000). Spatial use patterns, seasonal habitat selection, and interactions among adult gray foxes in Mississippi. *The Journal of Wildlife Management* 64(3): 742–751.

Chamberlain, M.J. & B.D. Leopold (2002). Movements and space use of gray foxes (*Urocyon cinereoargenteus*) following mate loss. *The American Midland Naturalist* 147(2): 409–412.

Chamberlain, M.J. & B.D. Leopold (2005). Overlap in space use among bobcats (*Lynx rufus*), coyotes (*Canis latrans*) and Gray Foxes (*Urocyon cinereoargenteus*). *American Midland Naturalist* 153(1): 171–179.

Cherry, M.J., K.L. Turner, M.B. Howze, B.S. Cohen, L.M. Conner & R.J. Warren (2016). Coyote diets in a longleaf pine ecosystem. *Wildlife Biology* 22(2): 64–70. https://doi.org/10.2981/wlb.00144

Constible, J.M., M. Chamberlain & B.D. Leopold (2006). Relationships between landscape pattern and space use of three mammalian carnivores in central Mississippi. *American Midland Naturalist* 155(2): 252–362.

Cooper, S.E., C.K. Nielsen & P.T. McDonald (2012). Landscape factors affecting relative abundance of gray foxes (*Urocyon cinereoargenteus)* at large scales in Illinois, USA. *Wildlife Biology* 18(4): 366–373. https://doi.org/10.2981/11-093

Cortés–Marcial, M., Y.M. Martínez Ayón & M. Briones–Salas (2014). Diversity of large and medium mammals in Juchitan, Isthmus of Tehuantepec, Oaxaca, Mexico. *Animal Biodiversity and Conservation* 37(1): 1–12. https://doi.org/10.32800/abc.2014.37.0001

Cunningham, S.C., L. Kirkendall & W. Ballard (2006). Gray fox and coyote abundance and diet responses after a wildfire in central Arizona. *Western North American Naturalist* 66(2): 169–180. https://doi.org/10.3398/1527-0904(2006)66[169:GFACAA]2.0.CO;2

Davis, M.L., M.J. Kelly & D.F. Stauffer (2011). Carnivore co-existence and habitat use in the Mountain Pine Ridge Forest Reserve, Belize. *Animal Conservation* 14(1): 56–65. https://doi.org/10.1111/j.1469-1795.2010.00389.x

Deuel, N.R., L.M. Conner, K.V. Miller, M.J. Chamberlain, M.J. Cherry & L.V. Tannenbaum (2017). Gray fox home range, spatial overlap, mated pair interactions and extra-territorial forays in southwestern Georgia, USA. *Wildlife Biology* https://doi.org/10.2981/wlb.00326

Donadio, E. & S.W. Buskirk (2006). Diet, morphology, and interspecific killing in carnivora. *American Naturalist* 167(4): 524–536. https://doi.org/10.1086/501033

Downey, P.J., E.C. Hellgren, A. Caso, S. Carvajal & K. Frangioso (2007). Hair snares for noninvasive sampling of felids in North America: do gray foxes affect success? *The Journal of Wildlife Management* 71(6): 2090–2094. https://doi.org/10.2193/2006-500

Elbroch, L.M. & M.L. Allen (2013). Prey indices and behaviors at a Gray Fox den in San Mateo County, California. *Western North American Naturalist* 73(2): 240–243. https://doi.org/10.3398/064.073.0215

Eriksson, C.E., K.M. Moriarty, M.A. Linnell & T. Levi (2019). Biotic factors influencing the unexpected distribution of a Humboldt marten (*Martes caurina humboldtensis*) population in a young coastal forest. *PLOS ONE* 14: e0214653. https://doi.org/10.1371/journal.pone.0214653

Farias, V., T.K. Fuller, R.K. Wayne & R.M. Sauvajot (2005). Survival and cause-specific mortality of gray foxes (*Urocyon cinereoargenteus*) in southern California. *Journal of Zoology* 266(3): 249–254. https://doi.org/10.1017/S0952836905006850

Farías, V., T.K. Fuller & R.M. Sauvajot (2012). Activity and distribution of Gray Foxes (*Urocyon cinereoargenteus*) in southern California. *The Southwestern Naturalist* 57(2): 176–181. https://doi.org/10.1894/0038-4909-57.2.176

Fedriani, J.M., T.K. Fuller, R.M. Sauvajot & E.C. York (2000). Competition and intraguild predation among three sympatric carnivores. *Oecologia* 125(2): 258–270. https://doi.org/10.1007/s004420000448

Fritzell, E. K. & K.J. Haroldson (1982). *Urocyon cinereoargenteus. Mammalian Species* 189: 1–8.

Fuller, T.K. & B. Cypher (2004). Gray Fox (*Urocyon cinereoargenteus*), pp. 92–97. In: Sillero-Zubiri, C., M. Hoffmann & D.W. Macdonald (eds). *Canids: Foxes, Wolves, Jackals, and Dogs—Status Survey and Conservation Action Plan*. IUCN/SSP Canid Specialist Group, Gland, Switzerland; and Cambridge, United Kingdom.

Gallina, S., P. Lopez-Colunga, C. Valdespino & V. Farias (2016). Relative abundance of the gray fox *Urocyon cinereoargenteus* (Carnivora: Canidae) in Veracruz central area, Mexico. *Revista De Biologia Tropical* 64(1): 221–233. https://doi.org/10.15517/rbt.v64i1.18237

Gehrt, S.D., S.P.D. Riley & B.L. Cypher (eds.) (2010). *Urban Carnivores: Ecology, Conflict, and Conservation*. The John Hopkins University Press, Baltimore, USA, 304pp.

Glenn, J.L.W., D.J. Civitello & S.L. Lance (2009). Multiple paternity and kinship in the gray fox (*Urocyon cinereoargenteus*). *Mammalian Biology* 74(5): 394–402. https://doi.org/10.1016/j.mambio.2008.10.003

Gompper, M.E. (2002). Top carnivores in the suburbs? Ecological and conservation issues raised by colonization of north-eastern North America by coyotes. *Bioscience* 52(2): 185–190. https://doi.org/10.1641/0006-3568(2002)052[0185:TCITSE]2.0.CO;2

Green, D.S., S.M. Matthews, R.C. Swiers, R.L. Callas, J.S. Yaeger, S.L. Farber, M.K. Schwartz & R.A. Powell (2018). Dynamic occupancy modelling reveals a hierarchy of competition among fishers, grey foxes and ringtails. *Journal of Animal Ecology* 87(3): 813–824. https://doi.org/10.1111/1365-2656.12791

Gómez-Ortiz, Y., O. Monroy-Vilchis & I. Castro-Arellano (2019). Temporal coexistence in a carnivore assemblage from central Mexico: temporal-domain dependence. *Mammal Research* 64(3): 333–342. https://doi.org/10.1007/s13364-019-00415-8

Greenberg, C.H. & M.R. Pelton (1994). Home range and activity patterns by Gray Foxes, *Urocyon cinereoargenteus* (Carnivorea: Canidae), in east Tennessee. *Brimleyana* 21: 131–140.

Haines, A.M., M.E. Tewes, L.L. Laack, J.S. Horne & J.H. Young (2006). A habitat-based population viability analysis for ocelots (*Leopardus pardalis*) in the United States. *Biological Conservation* 132(4): 424–436. https://doi.org/10.1016/j.biocon.2006.04.035

Harmsen, B.J., E. Sanchez, O.A. Figueroa, S.M. Gutierrez, C.P. Doncaster & R.J. Foster (2019). Ecology of a versatile canid in the Neotropics: gray foxes (*Urocyon cinereoargenteus*) in Belize, Central America. *Mammal Research* 64(3): 319–332. https://doi.org/10.1007/s13364-018-00413-2

Harrison, R.L. (1993). A survey of anthropogenic ecological factors potentially affecting gray foxes (*Urocyon cinereoargenteus*) in a rural residential area. *Southwestern Naturalist* 38(4): 352–356. https://doi.org/10.1656/058.011.0313

Harrison, R.L. (1997). A comparison of gray fox ecology between residential and undeveloped rural landscapes. *Journal of Wildlife Management* 61(1): 112–122. https://doi.org/10.2307/3802420

Harrison, R.L. (2002). Estimating gray fox home-range size using half-night observation periods. *Wildlife Society Bulletin* 30(4): 1273–1275.

Henke, S.E. & F.C. Bryant (1999). Effects of coyote removal on the faunal community in western Texas. *Journal of Wildlife Management* 63(4): 1066–1081.

Hody, J.W. & R. Kays (2018). Mapping the expansion of coyotes (*Canis* *latrans*) across North and Central America. *Zookeys* 759: 81–97. https://doi.org/10.3897/zookeys.759.15149

Holmgren, M. & S.A. Schnitzer (2004). Science on the rise in developing countries. *PLoS Biology* 2(1): 10–13. https://doi.org/10.1371/journal.pbio.0020001

Hostetler, J.A., J.W. McCown, E.P. Garrison, A.M. Neils, M.A. Barrett, M.E. Sunquist, S.L. Simek & M.K. Oli (2009). Demographic consequences of anthropogenic influences: Florida black bears in north-central Florida. *Biological Conservation* 142(11): 2456–2463. https://doi.org/10.1016/j.biocon.2009.05.029

Jones, G.D. & J.K. Frey (2008). First record of the gray fox (*Urocyon cinereoargenteus*) on Texas Barrier Islands. *Texas Journal of Science* 60(3): 225–227.

Kapfer, J.M. & R.W. Kirk (2012). Observations of gray foxes (*Urocyon cinereoargenteus*) in a suburban landscape in the piedmont of North Carolina. *Southeastern Naturalist* 11(3): 507–516. https://doi.org/10.1656/058.011.0313

Karlin, M. & G. De La Paz (2015). Using camera-trap technology to improve undergraduate education and citizen-science contributions in wildlife research. *Southwestern Naturalist* 60: 171–179. https://doi.org/10.1894/SWNAT-D-14-00005.1

Kelly, T.R. & J.M. Sleeman (2003). Morbidity and mortality of red foxes (*Vulpes vulpes*) and gray foxes (*Urocyon cinereoargenteus*) admitted to the Wildlife Center of Virginia, 1993–2001. *Journal of Wildlife Diseases* 39: 467–469. https://doi.org/10.7589/0090-3558-39.2.467

Klymus, K.E., C.A. Richter, N. Thompson & J.E. Hinck (2017). Metabarcoding of environmental DNA samples to explore the use of uranium mine containment ponds as a water source for wildlife. *Diversity* 9: 54. https://doi.org/10.3390/d9040054

Kowalski, B., F. Watson, C. Garza & B. Delgado (2015). Effects of landscape covariates on the distribution and detection probabilities of mammalian carnivores. *Journal of Mammalogy* 96: 511–521. https://doi.org/10.1093/jmammal/gyv056

LeFlore, E.G., T.K. Fuller, J.T. Finn, S. DeStefano & J.F. Organ (2019). Wild canid distribution and co-existence in a natural-urban matrix of the pioneer valley of western Massachusetts. *Northeastern Naturalist* 26: 325–342. https://doi.org/10.1656/045.026.0208

Lesmeister, D.B., C.K. Nielsen, E.M. Schauber & E.C. Hellgren (2015). Spatial and temporal structure of a mesocarnivore guild in midwestern North America. *Wildlife Monographs* 191: 1–61. https://doi.org/10.1002/wmon.1015

Lombardi, J.V., C.E. Comer, D.G. Scognamillo & W.C. Conway (2017). Coyote, fox, and bobcat response to anthropogenic and natural landscape features in a small urban area. *Urban Ecosystems* 20: 1239–1248. https://doi.org/10.1007/s11252-017-0676-z

Lovell, C.D., B.D. Leopold & C.C. Shropshire (1998). Trends in Mississippi predator populations, 1980-1995. *Wildlife Society Bulletin* 26: 552–556.

Mahard, T.J., J.A. Litvaitis, P. Tate, G.C. Reed & D.J.A. Broman (2016). An evaluation of hunter surveys to monitor relative abundance of bobcats. *Wildlife Society Bulletin* 40(2): 224–232.

Markovchick-Nicholls, L., H.M. Regan, D.H. Deutschman, A. Widyanata, B. Martin, L. Noreke & T.A. Hunt (2008). Relationships between human disturbance and wildlife land use in urban habitat fragments. *Conservation Biology* 22: 99–109. https://doi.org/10.1111/j.1523-1739.2007.00846.x

Maxwell, D. & S. Jennings (2005). Power of monitoring programmes to detect decline and recovery of rare and vulnerable fish. *Journal of Applied Ecology* 42(1): 25–37. https://doi.org/10.1111/j.1365-2664.2005.01000.x

Mcalpine, D., J.D. Martin & C. Libby (2008). First occurrence of the grey fox, *Urocyon cinereoargenteus*, in New Brunswick: a climate-change mediated range expansion? *Canadian Field-Naturalist* 122: 169–171.

Mella-Méndez, I., R. Flores-Peredo, J. Pérez-Torres, S. Hernández-González, D.U. González-Uribe & B.D. Bolivar-Cimé (2019). Activity patterns and temporal niche partitioning of dogs and medium-sized wild mammals in urban parks of Xalapa, Mexico. *Urban Ecosystems* 22: 1061–1070. https://doi.org/10.1007/s11252-019-00878-2

Moore, J.E., (1952). The gray fox in Alberta. *Journal of Mammalogy* 33: 253–253.

Mueller, M.M., D. Drake & M.L. Allen (2019). Using citizen science to inform urban canid management. *Landscape and Urban Planning* 189: 362–371. https://doi.org/10.1016/j.landurbplan.2019.04.023

Mumme, R.L., S.J. Schoech, G.W. Woolfenden & J.W. Fitzpatrick (2000). Life and death in the fast lane: demographic consequences of road mortality in the Florida scrub jay. *Conservation Biology* 14: 501–512. https://doi.org/10.1046/j.1523-1739.2000.98370.x

Nickel, B.A., J. Suraci, M.L. Allen & C.C. Wilmers (2020). Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biological Conservation* 241: 108383. https://doi.org/10.1016/j.biocon.2019.108383

O'Donnell, K. & J. delBarco-Trillo (2020). Changes in the home range sizes of terrestrial vertebrates in response to urban disturbance: a meta-analysis. *Journal of Urban Ecology* 6: 1–8. https://doi.org/10.1644/09-MAMM-A-312.1

Omernik, J.M. & G.E. Griffith (2014). Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. *Environmental Management* 54: 1249–1266. https://doi.org/10.1007/s00267-014-0364-1

Ordeñana, M.A., K.R. Crooks, E.E. Boydston, R.N. Fisher, L.M. Lyren, S. Siudyla, C.D. Haas, S. Harris, S.A. Hathaway, G.M. Turschak, A.K. Miles & D.H. van Vuren (2010). Effects of urbanization on carnivore species distribution and richness. *Journal of Mammalogy* 91: 1322–1331.

Pearman-Gillman, S.B., J.E. Katz, R.M. Mickey, J.D. Murdoch & T.M. Donovan (2020). Predicting wildlife distribution patterns in New England USA with expert elicitation techniques. *Global Ecology and Conservation* 21: e00853. https://doi.org/10.1016/j.gecco.2019.e00853

Perez-Solano, L.A., M. Gonzalez, E. Lopez-Tello & S. Mandujano (2018). Medium and large mammals associated with the tropical dry forest of central Mexico. *Revista De Biologia Tropical* 66: 1232–1243.

Peterson, R.L., R.O. Standfield, E.H. McEwen & A.C. Brooks (1953). Early records of the red and gray fox in Ontario. *Journal of Mammalogy* 34: 126–127.

Pineda-Guerrero, A., J.F. Gonzalez-Maya & J. Perez-Torres (2015). Conservation value of forest fragments for medium-sized carnivores in a silvopastoral system in Colombia. *Mammalia* 79: 115–119. https://doi.org/10.1515/mammalia-2013-0050

Reed, S.E. (2011). Non-invasive methods to assess co-occurrence of mammalian carnivores. *Southwestern Naturalist* 56: 231–240. https://doi.org/10.1894/F13-JKF-14.1

Rich, M., C. Thompson, S. Prange & V.D. Popescu (2018). Relative importance of habitat characteristics and interspecific relations in determining terrestrial carnivore occurrence. *Frontiers in Ecology and Evolution* 6: 1–13. https://doi.org/10.3389/fevo.2018.00078

Richmond, N.D. (1952). Fluctuations in gray fox population in Pennsylvania and their relationship to precipitation. *Journal of Wildlife Management* 16: 198–206. https://doi.org/10.2307/3796930

Riley, S.P.D. (2006). Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. *The Journal of Wildlife Management* 70: 1425–1435.

Riley, S.P.D., R.M. Sauvajot, T.K. Fuller, E.C. York, D.A. Kamradt, C. Bromley & R.K. Wayne (2003). Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology* 17: 566–576. https://doi.org/10.1046/j.1523-1739.2003.01458.x

Roemer, G., B. Cypher & R. List (2016). *Urocyon cinereoargenteus*. *The IUCN Red List of Threatened Species 2016*: e.T22780A46178068.

Rota, C.T., M.A.R. Ferreira, R.W. Kays, T.D. Forrester, E.L. Kalies, W.J. McShea, A.W. Parsons & J.J. Millspaugh (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution* 7: 1164–1173. https://doi.org/10.1111/2041-210X.12587

Sawyer, D.T. & T.T. Fendley (1994). Seasonal habitat use by gray foxes on the Savannah River site. *Proceedings of the Forty-Eighth Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 162–172.

Schantz, V.S. (1950). The gray fox in North-Dakota. *Journal of Mammalogy* 31: 197–198.

Schuler, K.L., G.M. Schroeder, J.A. Jenks & J.G. Kie (2014). Ad hoc smoothing parameter performance in kernel estimates of GPS-derived home ranges. *Wildlife Biology* 20: 259–266. https://doi.org/10.2981/wlb.12117

Schwertner, T.W., M.J. Peterson & N.J. Silvy (2006). Multi-scale asynchrony and spatial structuring of mesopredator abundance trends in central Texas, 1978–2003. *Texas Journal of Science* 58: 155–168.

Sillero-Zubiri, C., M. Hoffmann & D.W. Macdonald (2004). Canids: foxes, wolves, jackals and dogs. *Status Survey and Conservation Action Plan*. IUCN/SSC Canid Specialist Group. Gland, Switzerland.

Swaisgood, R.R., D. Wang & F. Wei (2018). Panda downlisted but not out of the woods. *Conservation Letters* 11: e12355.

Temple, D.L., M.J. Chamberlain & L.M. Conner (2010). Spatial ecology, survival and cause-specific mortality of gray foxes (*Urocyon cinereoargenteus*) in a longleaf pine ecosystem. *The American Midland Naturalist* 163: 413–422. https://doi.org/10.1674/0003-0031-163.2.413

Trapp, G.R. (1978). Comparative behavioral ecology of ringtail and gray fox in southwestern Utah. *Carnivore* 1: 3–32.

Walk, J.W., M.P. Ward, T.J. Benson, J.L. Deppe, S. Lischka, S.D. Bailey & J.D. Brawn (2010). Illinois birds: a century of change. Illinois Natural History Survey Special Publication 31, Champaign, USA.

Walters, J.R., S.R. Derrickson, M.D. Fry, S.M. Haig, J.M. Marzluff & J.M., Wunderle Jr. (2010). Status of the California condor (*Gymnogyps californianus*) and efforts to achieve its recovery. *The Auk* 127: 969–1001. https://doi.org/10.1525/auk.2010.127.4.969

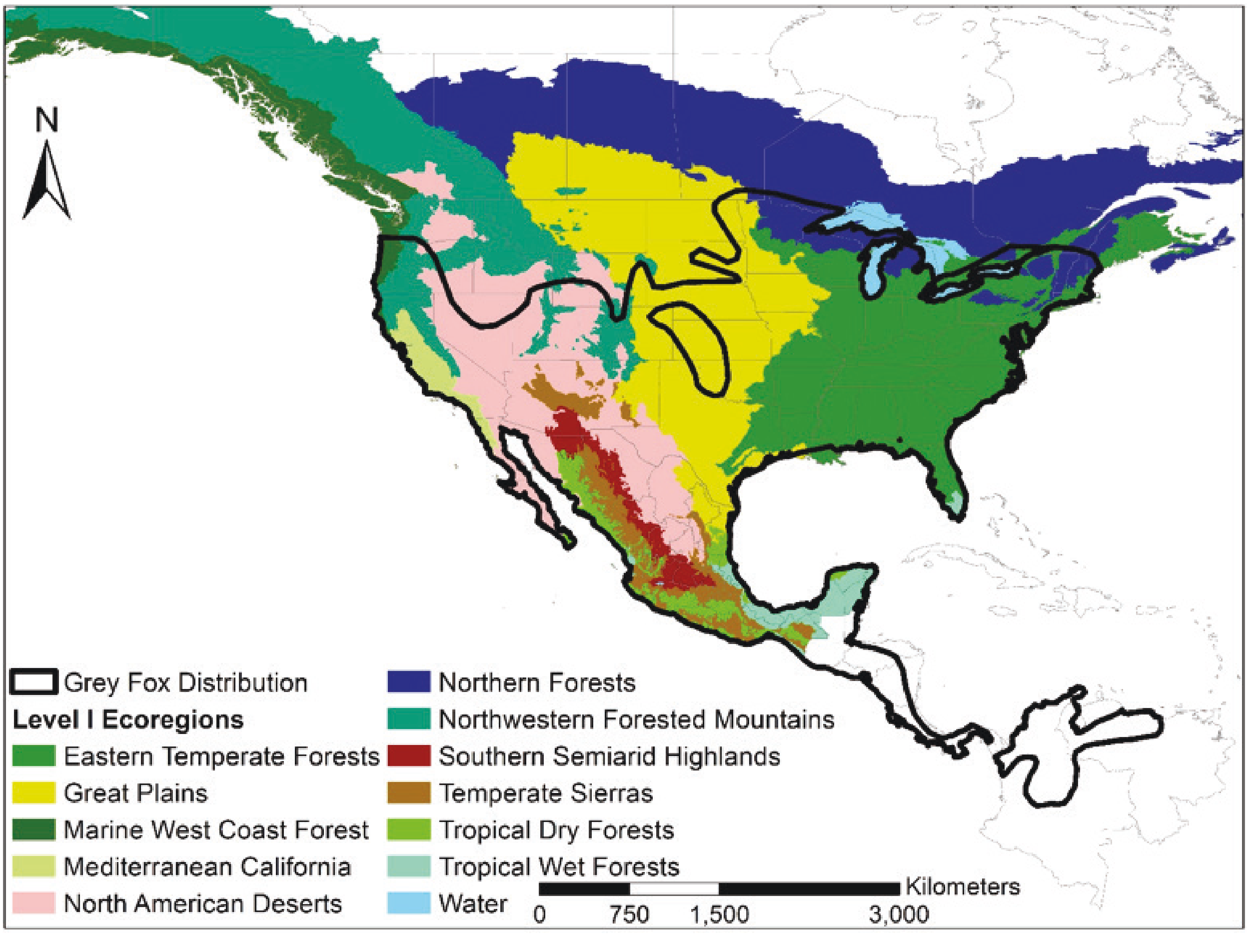
Walton, Z., G. Samelius, M. Odden & T. Willebrand (2017). Variation in home range size of red foxes *Vulpes vulpes* along a gradient of productivity and human landscape alteration. *PLoS ONE* 12: e0175291. https://doi.org/10.1371/journal.pone.0175291

Wang, Y., M.L. Allen & C.C. Wilmers (2015). Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biological Conservation* 190: 23–33. https://doi.org/10.1016/j.biocon.2015.05.007

Ward, R.J., R.A. Griffiths, J.W. Wilkinson & N. Cornish (2017). Optimising monitoring efforts for secretive snakes: a comparison of occupancy and N-mixture models for assessment of population status. *Scientific Reports* 7(1): 18074. https://doi.org/10.1038/s41598-017-18343-5

Weston, J.L. & I.L. Brisbin (2003). Demographics of a protected population of gray foxes (*Urocyon cinereoargenteus*) in South Carolina. *Journal of Mammalogy* 84: 996–1005. https://doi.org/10.1644/BOS-037

Zielinski, W.J., R.L. Truex, F.V. Schlexer, L.A. Campbell & C. Carroll (2005). Historical and contemporary distributions of carnivores in forests of the Sierra Nevada, California, USA. *Journal of Biogeography* 32: 1385–1407. https://doi.org/10.1111/j.1365-2699.2005.01234.x



Appendix 1. Level I ecoregions from Omernik & Griffith (2014) within our study area overlaid with the distribution of Grey Foxes (Roemer et al. 2016).

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