

# ECOGRAPHY

## Research article

### The differential contribution of coyotes and passerines on future biotic carbon storage through juniper seed dispersal

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Ecography

2024: e06958

doi: [10.1111/ecog.06958](https://doi.org/10.1111/ecog.06958)

Subject Editor:

Christine N. Meynard

Editor-in-Chief: Miguel Araújo

Accepted 18 December 2023



Differences in seed dispersal patterns can alter plant distributions, species persistence, plant community composition, and biotic carbon sequestered within a 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. This gap is important to understand because carnivorans may be better suited to assist plant dispersal in disturbed habitats and the longer distances necessary for climate migration. In this study, we evaluated how seed dispersal by a particular carnivoran, coyote *Canis latrans*, differed from passerines *Passeriformes* for juniper *Juniperus* sp. in the conterminous 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, and then using climate predictions to define spatial changes in suitable niches. Seed dispersal by both coyote and passerine dispersers was simulated to estimate total juniper dispersal, juniper encroachment into grasslands, and finally changes in above-ground biotic carbon storage due to juniper encroachment. Our models indicate that over the next 80 years, suitable conditions for juniper will contract, but losses from the current range will be minimal. Our model suggests that coyote dispersal of juniper will result in a 54–59% increase in range, which is 2.5 times as much as the estimated increase provided by passerines. We estimate that coyotes will facilitate juniper encroachment into 170 000–185 000 km<sup>2</sup> of current grasslands, 3.4 times as much as passerines. Modeling the effect of coyote-mediated juniper encroachment of grasslands, we forecast that the addition of woody aboveground biomass will provide between 1.1 and 1.2 Pg of additional carbon storage over the next 80 years. Results highlight how coyotes and passerines provide different outcomes for changes in juniper ranges, plant community composition, and landscape carbon storage. Understanding the differences in outcomes provided by different seed dispersers is important for modeling plant species distributions and carbon storage.

Keywords: carbon storage, climate change, coyote, grassland encroachment, juniper, seed dispersal



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## 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 and pathogens near conspecific plants (Janzen 1970, Connell 1971, Comita et al. 2014). 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 in terms of the quantity of seeds dispersed and the quality of deposition sites for plant performance (Schupp et al. 2010) influences plant community composition and ultimately ecosystem functioning, such as landscape-level biotic carbon storage (Bello et al. 2015).

Plants have evolved multiple mechanisms to mediate seed dispersal, including structures surrounding and adjacent to seeds that influence the effectiveness of dispersal by wind, water, or animal vectors (Schupp et al. 2010). Some plant species produce fruit that attract a frugivore, which then disperses the seed via regurgitation or defecation, termed endozoochory; however, even plants without specific adaptations for dispersal by frugivores can be dispersed by animals (Beckman and Sullivan 2023). Endozoochory aids seeds by dispersing them away from the parent plant which improves seedling establishment and population connectivity and can increase the potential for the seed to be deposited in spatially disjunct suitable sites necessary for recruitment (i.e. directed dispersal, Grubb 1977, Higginbotham 1993, Hohnung-Gaese 2007). Endozoochory can provide effective seed dispersal by dispersing a large quantity of seeds to habitats suitable for plant survival and growth (sensu Schupp et al. 2010).

Birds and mammals provide important seed dispersal services. Within these classes, passerines Passeriformes and carnivores Carnivora, are particularly important seed dispersers in North America (Willson 1993, Stiles 2000). Both passerines and carnivores 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 (Escribano-Avila et al. 2014). Passerines tend to consume seeds and disperse them within a contiguous forest or brushy patch with ample perches resulting in relatively short dispersal distances (Herrera and García 2010). Conversely, carnivores tend to deposit seeds at greater distances from the mother tree (González-Varo et al. 2013, Suárez-Esteban et al. 2013, Escribano-Avila et al. 2014, Rubalcava-Castillo et al. 2020). Shorter realized dispersal distances by passerines likely ensure seed establish in suitable habitat, whereas longer realized dispersal distances provided by carnivores may improve population connectivity and the ability of plants to establish in newly suitable sites that are separated from their current range (Rost et al. 2012, Fedriani et al. 2018).

Climate change is altering the spatial distribution of ecological niches or the suitable conditions necessary for the survival and reproduction of many plant species. Such changes in the ecological niche can result in species range shifts (e.g. contractions and expansions; Lenoir and Svenning 2015). In response to changes in climate conditions relevant to a plant's ecological niche, plant populations will need to either adapt or track suitable conditions via dispersal, 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 and Murrell 2003), which in turn can facilitate adaption to perturbations caused by climate change (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 and Westcott 2013, Fricke et al. 2022). Both in situ adaptation and population range shifts benefit from the dispersal distance provided by seed dispersal partners, hence, understanding the differences between different dispersal partners is important to understanding future plant community distributions (González-Varo et al. 2021).

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 plant genera (Draper et al. 2022). In addition to coyotes being a prolific fruit- and seed-consuming species throughout their range (Jensen et al. 2022) coyote consumption of seeds and subsequent gut passage have no negative effects on seed viability (Stevens et al. 2020, Draper et al. 2021). Coyotes live in diverse habitats, which has contributed to their rapid range expansion of over 40% in the last 70 years (Hody and Kays 2018). This range expansion has created new seed dispersal mutualisms (Roehm and Moran 2013) which may be particularly important for plants tracking climate change (Fricke et al. 2022). Additionally, this provides an interesting comparison to studies that focused on the effect of defaunation on seed dispersal and biotic carbon storage (Bello et al. 2015, Peres et al. 2016, Culot et al. 2017, Rogers et al. 2021). Changes in plant communities can alter a landscape's gross carbon storage through changes in the size of individual plants and biomass allocation to different plant tissues.

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 species are expanding their distributions worldwide in response to changing landscapes and climate conditions (García et al. 2014, Filippelli et al. 2020). In North America, these expansions are due in part to the increased susceptibility of grasslands to conversion caused by livestock grazing and changes in fire regimes (Filippelli et al. 2020). This encroachment alters critical habitats for threatened and endangered species (Van Auken 2009, Caracciolo et al. 2017, Coates et al. 2017). 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 aboveground carbon storage through their wood structures ([Fernandez et al. 2013](#), [Throop and Lajtha 2018](#)).

In this study, we modeled the expansion of juniper and its consequent 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 suitable habitats of multiple juniper species, then determined how different seed dispersal mutualists affected juniper expansion into these future suitable habitats. We utilized coyotes as the model species representing carnivores due to their prolific range expansion covering the entire conterminous United States ([Hody and Kays 2018](#)), generalist diets ([Lendrum 2017](#)), and known consumption of juniper fruits ([Schupp et al. 1997](#), [Chambers et al. 1999](#)), with seeds remaining viable after digestion ([Draper et al. 2021](#)). For comparison, we selected a representative community of passerines with well-documented consumption of juniper fruits, large contiguous ranges that co-occur with coyotes and juniper, and are not experiencing population declines ([Martin 1951](#), [Holthuijzen and Sharik 1985](#), [Chambers et al. 1999](#), [Sauer et al. 2014](#), [Longland and Dimitri 2016](#), [Stricklan et al. 2020](#)). The passerine assemblage included the American robin *Turdus migratorius*, cedar waxwing *Bombycilla cedrorum* and European starling *Sturnus vulgaris*, [Holthuijzen and Sharik 1985](#), [Chambers et al. 1999](#), [Stricklan et al. 2020](#)). We quantified how different patterns of dispersal between coyotes and these passerines would affect the 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.

## Material and methods

Four main data inputs were required to model the effect of different seed dispersal agents on aboveground biotic carbon storage: 1) species occurrence data for juniper species, 2) climate projections to define future conditions, 3) estimates of seed dispersal distances for avian species and coyotes 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 aboveground carbon storage for the conversion of grasslands to juniper as a result of dispersal by coyotes and passerines.

### Juniper occurrence

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 (FIA, [Forest Inventory and Analysis 2007](#)). We utilized publicly available fuzzed and swapped (minor

alterations of location data to protect landowner privacy as required by law) data because it has been shown to perform well at resolutions finer than the 2.5 km<sup>2</sup> 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. virginiana* occurring east of the Great Plains ([Forest Inventory and Analysis 2007](#)). All seven species produce a dry cone between 5 and 12 mm ([USDA and NRCS 2020](#)), which provides nourishment to passerine and coyote consumers who in general pass the seeds intact ([Holthuijzen and Adkisson 1984](#), [Draper et al. 2021](#)).

## Climate projections to define future projections

### Bioclimatic variables

Bioclimatic variables for current and future conditions were downloaded from WorldClim ([Fick and 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) 2.0-4.5 and 5.0-8.5, 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 record and merged these buffers within each species to provide a spatially appropriate region from which to draw background environmental data ([Barbet-Massin et al. 2012](#), [Merow et al. 2013](#), [Phillips et al. 2017](#)). Environmental and climate data was sampled at a 2.5 km resolution to accommodate a common resolution between all data sets and accommodate the limitations of the fuzzed and swapped FIA data. For this project, our primary focus was understanding the influence of dispersal differences on distributions rather than forecasting future distributions. Therefore, we opted for a streamlined approach, using a single model for ecological niche modeling. 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](#)). For each species, we used 100 cross-validation replicates, training the model on 70% of the data and evaluating it using a receiver operator curve (ROC). All presence-absence and suitability estimates were derived from a final model run using the

full data. All presence-absence and suitability estimates were drawn from a final model run with the complete data set (settings and code available in the Supporting information). 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, resulting in an end projection 80 years in the future) and under two SSPs scenarios (2.0-4.5 and 5.0-8.5) for the full extent of the conterminous US ([Fig. 1](#)).

## Seed dispersal distances

### Seed dispersers

We considered seed dispersal by a representative assemblage of passerines considered to be the most prolific avian consumers of juniper ([Holthuijzen and Sharik 1985](#), [Chambers et al. 1999](#)). Observed dispersal by passerines showed an average dispersal between 12 and 40 m for junipers ([Holthuijzen and Sharik 1985](#), [Chavez-Ramirez and Slack 1994](#)). Dispersal distances for passerines may range further based on gut-passage time (~ 12–30 min; [Holthuijzen and Adkisson 1984](#), [Bartuszevige and Gorchov 2006](#)); however, post-consumption behavior and digestion by birds suggest such dispersal would occur only as rare long-distance dispersal events ([Holthuijzen and Sharik 1985](#), [Chavez-Ramirez and Slack 1994](#), [Chambers et al. 1999](#), [Herrera and García 2010](#)). Therefore, we estimated that average passerine seed dispersal would be limited to suitable habitats that were immediately adjacent to established populations of juniper, with rare long-distance dispersal events.

In a captive setting, gut-passage time for coyotes consuming *J. osteosperma* averages between 8 and 24 h ([Draper et al. 2021](#)). Coyotes move ~ 0.94 km h<sup>-1</sup> on average ([Kitchen et al. 2000](#)) with a total displacement of 5.5–7.0 km over 24 h ([Young et al. 2006](#), [Chamberlain et al. 2021](#)). However, much of a coyote's movement is constrained to its home range which can average between 10.6 and 20.7 km<sup>2</sup> for resident coyotes and over 200 km<sup>2</sup> for transients ([Gifford et al. 2017](#), [Chamberlain et al. 2021](#)). Canid seed dispersal has also been shown to correlate with an animal's home range with maximum realized dispersal approaching the maximum distance available within their home range ([González-Varo et al. 2013](#)). Therefore, we estimated a dispersal ≤ 5 km to represent regular dispersal events, with the likelihood of dispersal decreasing as it approached the 5 km maximum. As with passerines, we included a rare long-distance dispersal parameter to account for seed dispersal that coincided with transient coyote dispersal. Although coyote home range size varies across habitats, we used a single dispersal kernel up to 5 km across all habitat types to accommodate computational limitations, and because it represents a conservative maximum dispersal distance. These dispersal distances will be used to define the dispersal neighborhood of a grid-based dispersal

model, with multiples of the resolution of the grids defining different potential dispersal step lengths.

### Model of animal-mediated dispersal of juniper

Differences in the dispersal potential of junipers between coyotes and passerines were modeled using the 'MigClim' package in R ([Engler and Guisan 2009](#), [Engler et al. 2012](#), [www.r-project.org](#)). We generated present-day occurrence maps for each plant species by using binary Maxent model predictions, which were chosen based on the optimization of the area under the ROC curve for current climate conditions. Estimates were constrained to the background buffers generated above for each species. All cells identified in the current occurrence map were assumed to contain stable mature stands. Maxent model forecasts provided habitat suitability maps with dispersal-independent occurrence probabilities for each time step and SSP for each species. Map resolution was increased to 1 km<sup>2</sup> to meet the needs of the cellular automata employed in MigClim. 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](#)); however, these landscapes were not treated as barriers because coyotes and passerines readily disperse through them ([Grubbs and Krausman 2009](#), [Gehrt and Brown 2011](#), [Larson et al. 2020](#)). Adult establishment was identified as a random event, influenced by both the probability of a seed dispersing into a cell and the probability of recruiting from a seed to an adult based on the suitability of a cell. We assumed suitability values provided by Maxent represented a comprehensive measure of the factors influencing a plant's growth, survival, and reproduction integrating across all stages of recruitment from the seed to the adult stages. Initial maturity for newly converted raster cells was set to 10 years and dispersal was modeled as only occurring on alternating years to match juniper ecology ([USDA and NRCS 2020](#)). All newly converted cells were assumed to have sufficient recruitment from the conversion 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. Passerine seed dispersal probabilities were set at 1 for dispersal of 1 km, a dispersal step of 1 km is substantially larger than observed avian seed dispersal but is the smallest unit at which a model of this scale could be run. Coyote dispersal probabilities were set to 1.0, 0.8, 0.6, 0.4 and 0.2 for 1, 2, 3, 4 and 5 km respectively, following the general trend in dispersal kernels observed in other canids ([González-Varo et al. 2013](#)). Dispersal estimates did not account for potential dispersal patterns during annual migrations. However, the model included a rare long-distance dispersal of between 10 and 20 km, the range of maximum dispersal distances given for average gut passage times and travel speeds of our model dispersers ([Holthuijzen and Adkisson 1984](#), [Draper et al. 2021](#)). This dispersal was modeled with a probability of 0.01, to allow for the inclusion of a rare long-distance dispersal

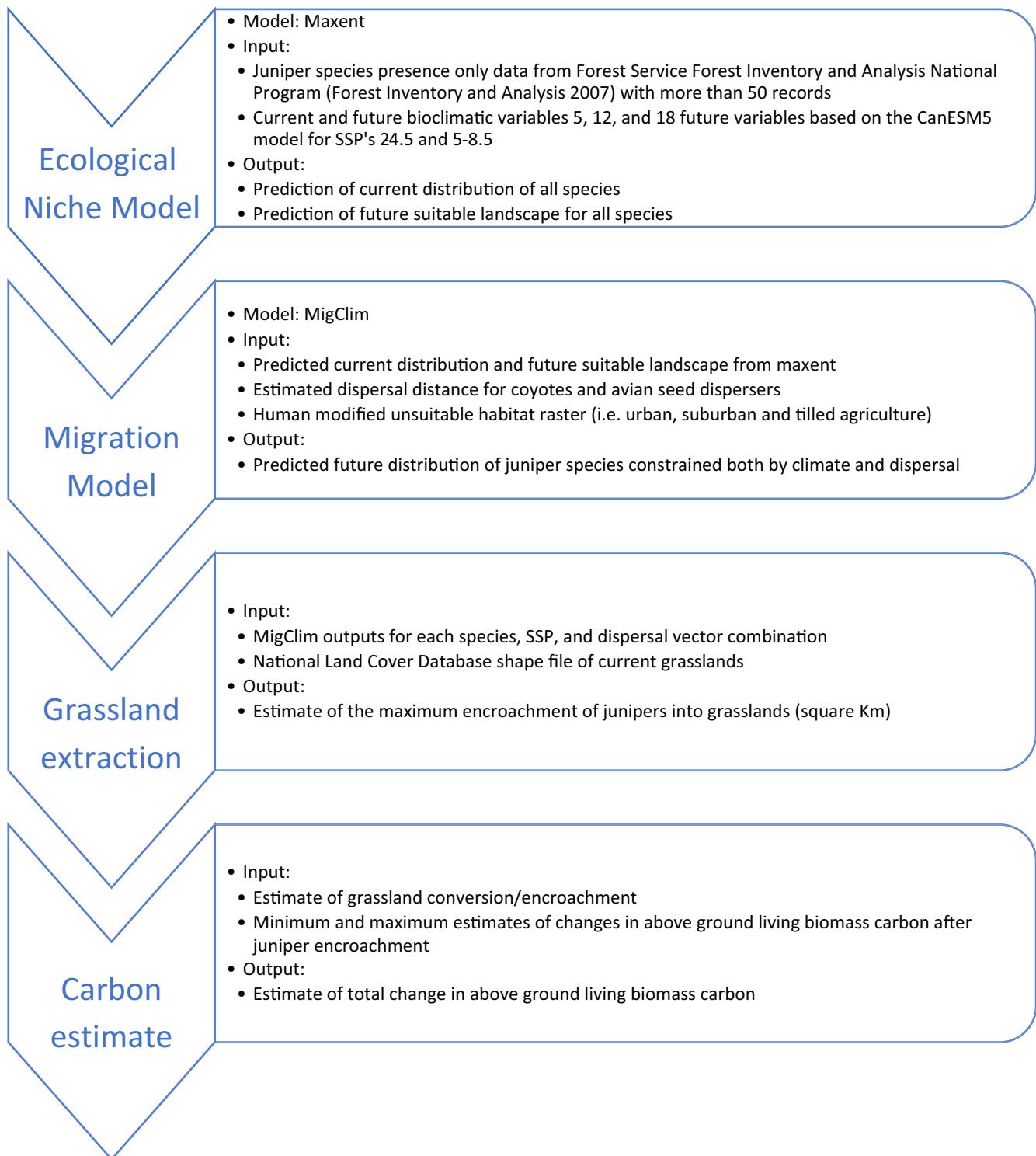


Figure 1. Flow chart of inputs and outputs of each modeling step in our analysis of juniper dispersal by two vertebrate seed dispersers, and the resulting rate of grassland encroachment and increases in above-ground biotic carbon storage under changing climate conditions.

event arising from the movement of transient coyotes, who can comprise  $6.4\% \pm 3.9$  of a population ([Berger and Gese 2007](#)). We ran 100 replicates for each combination of plant  $\times$  disperser  $\times$  SSP combination for four 20 year 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<sup>-6</sup> Pg increase, SE= 8.9<sup>-7</sup> Pg C; 1 Pg = 1 Gt) 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 × 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 the loss of juniper stands or the 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. The area under the curve for the receiver operator curves for the resulting Maxent models ranged between 0.80 and 0.94, and the Boyce index ranged between 0.93 and 1 (Supporting information). Current highly suitable climate conditions for juniper extend well beyond the observed and predicted ranges of juniper species. Under future climate scenarios, highly suitable conditions appear to be partially aligned with the current predicted range of juniper ([Fig. 2](#)). As the climate warms, suitable conditions advance upslope following a band of warmest month maximum temperature roughly between 20 and 35°C. 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 prior to estimating dispersal, with *J. deppeana*, *J. monosperma* and *J. scopulorum* having modest losses of their original ranges under SSP 2.0-4.5 (> 1%). Under SSP 5-8.5, *J. deppeana*, and *J. scopulorum* lost < 5% of their original range, while *J. monosperma* lost 26.25% of its original range between 2081 and 2100. These 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 passerine and coyote seed dispersers expanded modeled juniper ranges, offsetting any losses caused by climate change. Under SSP 2.0-4.5, junipers expanded between 24 and 59% (passerines and coyote dispersal respectively) of their total range, and under SSP 5.0-8.5, they expanded between 21 and 54% of their total range. 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 5.0-8.5, this species expanded its total range by 21 to 46% by 2100 when dispersers were included. 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. Modeling migration rates of juniper showed that coyotes consistently provided 2.5 times greater range expansion for junipers compared to passerines ([Fig. 3](#), Supporting information).

The difference in modeled dispersal between the two taxa was more pronounced for grassland conversion to juniper woodlands, where coyotes provided 3.4 times more conversion than their passerine counterparts (Supporting information). For SSP 2.0-4.5, coyotes converted over 185 000 km<sup>2</sup> of grasslands to juniper woodlands while passerines converted less than 55 000 km<sup>2</sup>. We found a similar trend between the two dispersers at SSP 5.0-8.5, albeit with less overall grassland conversion due to climate conditions being less suitable for juniper expansion (170 000 and ~ 49 000 km<sup>2</sup> 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 modeled 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 versus 1.2 ± 0.3 Pg C) more carbon storage on the landscape by 2100 under SSP 2.0-4.5 compared to when junipers were only dispersed by passerine species ([Fig. 4](#), Supporting information). Similarly, coyote-aided seed dispersal under SSP 5.0-8.5 resulted in 0.76 Pg C (0.32 ± 0.08 versus 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. scopulorum*, *J. osteosperma* and *J. occidentalis*) provided the largest contribution to grassland encroachment and increases in landscape-level carbon storage. *J. scopulorum* 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](#), [Rogers et al. 2021](#)). The distribution, composition, and populations of different

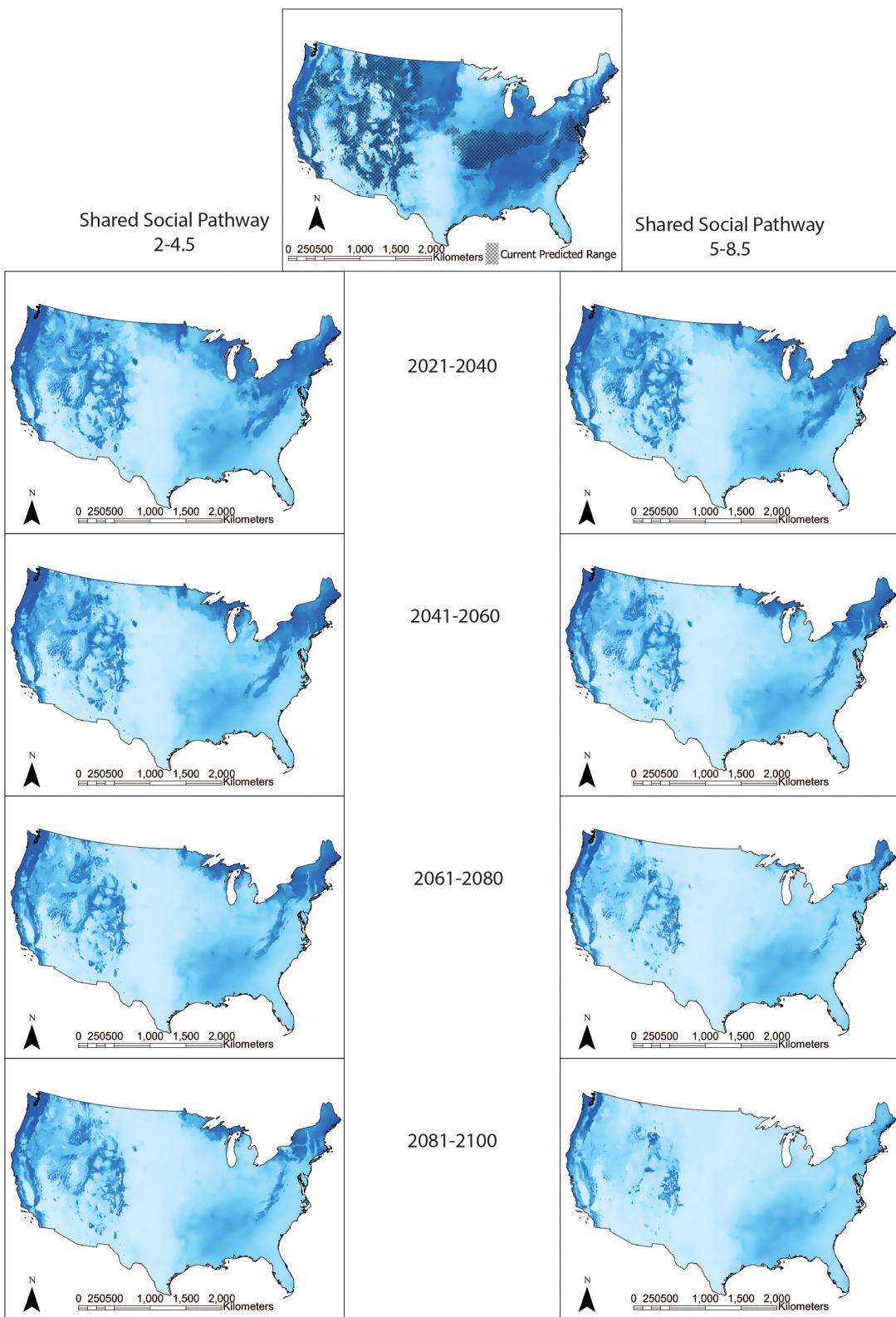


Figure 2. Ecological niche model results for seven species of juniper (*J. californica*, *J. deppeana*, *J. monosperma*, *J. occidentalis*, *J. Osteosperma*, *J. scopulorum* and *J. virginiana*), under two different climate change scenarios (SSP 2.0-4.5 and 5.0-8.5). The top map represents the currently 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. Maps represent the combined results for all seven species. Suitability for juniper advanced upslope and north tracking favorable temperatures, and away from mesic conditions due to narrow precipitation tolerances.

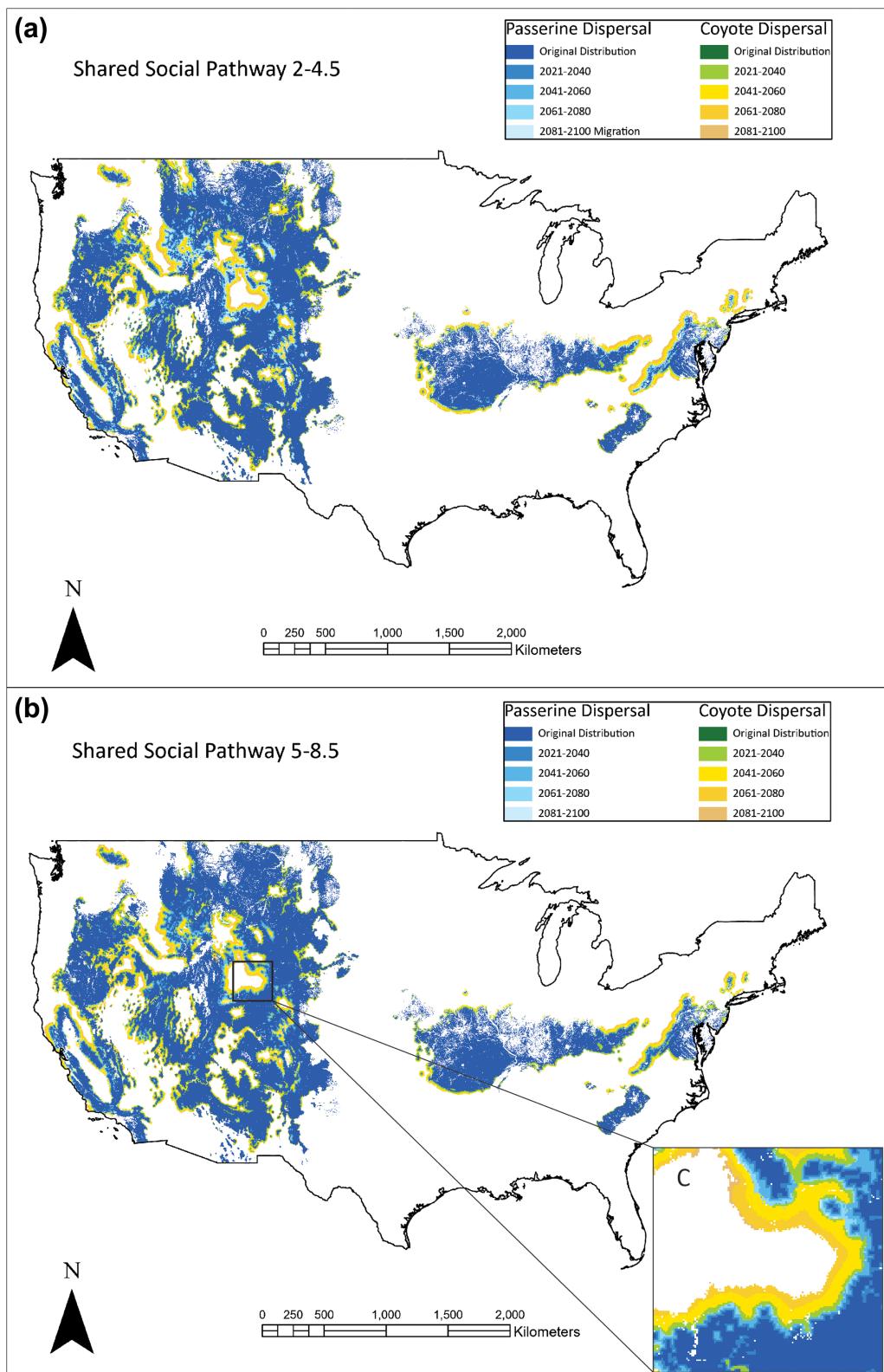


Figure 3. Juniper dispersal model results for dispersal by both coyotes (greens and yellows) and passerines (blues) across the conterminous United States from 2021–2100 under a moderate climate change scenario (Shared Social Pathway 2.0-4.5, panel (a)) and a severe climate change scenario (Shared Social Pathway 5.0-8.5, panel (b)). 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

Figure 3. Continued

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. (c) shows a close-up of where coyote dispersal extends well beyond avian dispersal for the first three timesteps achieving maximum dispersal until the final (4th) time step where dispersal is limited by ecological niche rather than dispersal capability.

dispersal guilds are changing. Within a given dispersal, guild members may be added or subtracted with changes in species distributions or an individual species' relative importance may change as its population density changes due to anthropogenic influences (Pedrosa et al. 2019, Fricke et al. 2022). 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. Our models estimate 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 (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 can help the seven juniper species 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 (Fig. 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 relative to passerines was 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 our model estimates, coyotes can convert 3.4 times ( $> 185,000$  versus  $< 55,000 \text{ km}^2$ , at SSP 2.0-4.5) more area of grassland than passerines. Elsewhere modeled 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 ( $970,000$  versus  $389,000 \text{ km}^2$  at SSP 2.0-4.5). Previous studies have documented 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  $\sim 3000 \text{ km}^2$  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

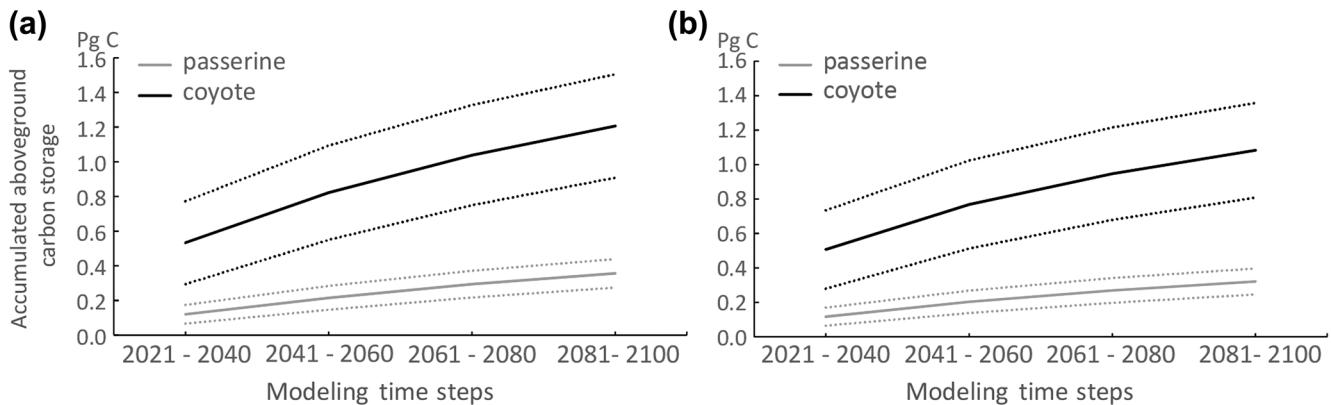


Figure 4. Gross new above-ground biotic carbon storage provided by passerine and coyote-mediated seed dispersals of junipers *Juniperus* sp. into grasslands. (a) shows changes predicted under SSP 2.0-4.5 and (b) shows changes predicted under SSP 5.0-8.5. Values are reported in Petagrams of carbon (Pg C) with 95% confidence intervals (dotted lines) that account for the cumulative error of all modeling steps.

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<sup>2</sup> or 0.05% respectively) provided by passerines under the same conditions suggest that juniper is dispersed by multiple unique seed dispersers that provide complementary dispersal services; otherwise, the previously observed rates of expansion would not be possible.

Our model found 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 estimates that future juniper encroachment will increase above-ground biotic carbon storage by 0.32–1.20 Pg C over the next 80 years. This estimate is also likely an underestimate of the total change in biotic carbon storage given that below-ground biotic carbon storage is likely to increase substantially as well (Barger et al. 2011, Fernandez et al. 2013). 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 (Fig. 4). Juniper encroachment into grasslands also increases the volume and proportion of biotic carbon deposited on the soil surface as litter 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 and Blair 2008, Throop and 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<sub>2</sub>. 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 the overall resilience of the landscape 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). For example, greater sage grouse *Centrocercus urophasianus*, a vulnerable species in the Intermountain West, are particularly susceptible to the ill effects of juniper encroachment because it reduces forage for sage grouse and 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 computational capabilities, uncertainties, and ecological factors that were beyond the scope of this study. First, given the spatial scale of this model and software and hardware limitations, the smallest spatial unit that could be considered was 1 km<sup>2</sup>. This scale has likely led to an overestimation of dispersal of juniper by passerines. Though this limits the utility of this model for fine-scale carbon estimates or localized spatial predictions for passerines, it provides useful insights into the potential impact of adding or removing under-studied, large-bodied seed dispersers. As our results are likely conservative in the differences between passerine and coyote dispersal, this only further highlights the potential importance of coyotes for carbon storage. Second, juniper is a heavily managed plant, and juniper encroachment into grasslands and other habitats is controlled through removal programs (Farzan et al. 2015, Bombaci and Pejchar 2016). Historical removal 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, including juniper removals, which may reduce the rate of juniper expansion and encroachment. Finally, our model only accounted for landscape permeability as it related to climate suitability, we did not include additional landscape variables and microsite features that could influence arrival of seeds (e.g. available perches for passerines, favorable travel corridors for coyotes), seed germination, and seed recruitment (e.g. differential effects of existing vegetation, nurse plants versus competitive exclusion, seed predation). Both grazing and fire are common occurrences in juniper habitats and grasslands that can also affect landscape permeability. 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 that adds biotic and abiotic filters, disperser behavior, and management would improve predictions obtained in our study of the expansion of juniper and its overall effects on the landscape. Additionally, our model was primarily conceptual to evaluate the effect of differential dispersal and we encourage the use of an ensemble model approach for defining niche suitability when forecasting species distributions (Valavi et al. 2022).

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 (Osuri et al. 2016, Chanthorn et al. 2019, Fricke et al. 2022). Our study 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. This furthers findings that novel introduced seed dispersers or those undergoing range expansions may be particularly important to climate migration for plants (Fricke et al. 2022). Our findings show that a diverse dispersal guild was important for helping junipers expand under moderate and severe climate change (Peres et al. 2016, Chanthorn et al. 2019). 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 carnivores in plant dispersal models.

**Acknowledgements** – We would like to thank E. Hammill and K. Kettenring for comments on an early version of this manuscript.

**Funding** – This research was funded by a Department of Watershed Sciences PhD Scholarship, a Utah State University (USU) Ecology Center Scholarship, and the USDA-National Wildlife Research Center. TA was funded by an Early Career Research Fellowship from the Gulf Research Program of the National Academies of Sciences, Engineering, and Medicine.

## Author contributions

**John P. Draper:** Conceptualization (equal); Data curation (lead); Formal analysis (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (equal). **Julie K. Young:** Conceptualization (equal); Funding acquisition (equal); Writing – review and editing (equal). **Noelle G. Beckman:** Conceptualization (equal); Writing – review and editing (equal). **Trisha B. Atwood:** Conceptualization (equal); Funding acquisition (equal); Writing – review and editing (equal).

## Data availability statement

All data used for this analysis was derived from open access sources available online; climate data: <https://www.worldclim.org/>, species occurrence data: <https://www.fs.usda.gov/research/programs/fia>, land cover data: <https://www.usgs.gov/centers/eros/science/national-land-cover-database>. Model code is available at the figshare repository: <https://doi.org/10.6084/m9.figshare.25062419>.

## Supporting information

The Supporting information associated with this article is available with the online version.

## References

- Barbet-Massin, M., Jiguet, F., Albert, C. H. and Thuiller, W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? – *Methods Ecol. Evol.* 3: 327–338.
- Barger, N. N., Archer, S. R., Campbell, J. L., Huang, C. Y., Morton, J. A. and Knapp, A. K. 2011. Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem carbon balance. – *J. Geophys. Res.* 116: 1–17.
- Bartuszevige, A. M. and Gorchov, D. L. 2006. Avian seed dispersal of an invasive shrub. – *Biol. Invas.* 8: 1013–1022.
- Beckman, N. G. and Sullivan, L. L. 2023. The causes and consequences of seed dispersal. – *Annu. Rev. Ecol. Evol. Syst.* 54: 403–427.
- Bello, C., Galetti, M., Pizo, M. A., Magnago, L. F. S., Rocha, M. F., Lima, R. A. F., Peres, C. A., Ovaskainen, O. and Jordano, P. 2015. Defaunation affects carbon storage in tropical forests. – *Sci. Adv.* 1: e1501105.
- Berger, K. M. and Gese, E. M. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? – *J. Anim. Ecol.* 76: 1075–1085.
- Bohrer, G., Nathan, R. and Volis, S. 2005. Effects of long-distance dispersal for metapopulation survival and genetic structure at ecological time and spatial scales. – *J. Ecol.* 93: 1029–1040.
- Bombaci, S. and Pejchar, L. 2016. Consequences of pinyon and juniper woodland reduction for wildlife in North America. – *For. Ecol. Manage.* 365: 34–50. <https://doi.org/10.1016/j.foreco.2016.01.018>
- Caracciolo, D., Istanbulluoglu, E. and Noto, L. V. 2017. An eco-hydrological cellular automata model investigation of juniper tree encroachment in a western North American landscape. – *Ecosystems* 20: 1104–1123.
- Chamberlain, M. J., Cohen, B. S., Wightman, P. H., Rushton, E. and Hinton, J. W. 2021. Fine-scale movements and behaviors of coyotes (*Canis latrans*) during their reproductive period. – *Ecol. Evol.* 11: 9575–9588.
- Chambers, J. C., Vander Wall, S. B. and Schupp, E. W. 1999. Seed and seedling ecology of piñon and juniper species in the Pygmy Woodlands of western North America. – *Bot. Rev.* 65: 1–38. <http://www.jstor.org/stable/4354335>
- 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: 10015.
- Chavez-Ramirez, F. and Slack, R. D. 1994. Effects of avian foraging and post-foraging behavior on seed dispersal patterns of Ashe juniper. – *Oikos* 71: 40–46.
- Chillo, V., Anand, M. and Ojeda, R. A. 2011. Assessing the use of functional diversity as a measure of ecological resilience in arid rangelands. – *Ecosystems* 14: 1168–1177.
- Coates, P. S., Prochazka, B. G., Ricca, M. A., Gustafson, K. B., Ben, Ziegler, P. and Casazza, M. L. 2017. Pinyon and juniper encroachment into sagebrush ecosystems impacts distribution and survival of greater sage-grouse. – *Rangel. Ecol. Manage.* 70: 25–38.
- Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., Beckman, N., Zhu, Y. and Gómez-Aparicio, L. 2014. Testing predictions of the Janzen–Connell hypothesis: a meta-analysis of experimental evidence for distance- and density-dependent seed and seedling survival. – *J. Ecol.* 102: 845–856.
- Connell, J. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. – *Dynam. Popul.* 298: 298–312.
- Corlett, R. T. and Westcott, D. A. 2013. Will plant movements keep up with climate change? – *Trends Ecol. Evol.* 28: 482–488.
- Culot, L., Bello, C., Batista, J. L. F., Do Couto, H. T. Z. and Galetti, M. 2017. Synergistic effects of seed disperser and pred-

- ator loss on recruitment success and long-term consequences for carbon stocks in tropical rainforests. – *Sci. Rep.* 7: 7662.
- Draper, J. P., Atwood, T. B., Beckman, N. G., Kettenring, K. M. and Young, J. K. 2021. Mesopredator frugivory has no effect on seed viability and emergence under experimental conditions. – *Ecosphere* 12: e03702.
- Draper, J. P., Young, J. K., Schupp, E. W., Beckman, N. G. and Atwood, T. B. 2022. Frugivory and seed dispersal by carnivores. – *Front. Ecol. Evol.* 10: 864864.
- Engler, R. and Guisan, A. 2009. MigClim: predicting plant distribution and dispersal in a changing climate. – *Divers. Distrib.* 15: 590–601.
- Engler, R., Hordijk, W. and Guisan, A. 2012. The MIGCLIM R package – seamless integration of dispersal constraints into projections of species distribution models. – *Ecography* 35: 872–878.
- Escribano-Avila, G., Calviño-Cancela, M., Piás, 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.
- Farzan, S., Young, D. J. N., Dedrick, A. G., Hamilton, M., Porse, E. C., Coates, P. S. and Sampson, G. 2015. Western juniper management: assessing strategies for improving greater sage-grouse habitat and rangeland productivity. – *Environ. Manage.* 56: 675–683. <https://doi.org/10.1007/s00267-015-0521-1>
- 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.
- Fernandez, D. P., Neff, J. C., Huang, C. Y., Asner, G. P. and Barger, N. N. 2013. Twentieth century carbon stock changes related to piñon-Juniper expansion into a black sagebrush community. – *Carbon Balance Manage.* 8: 8.
- Fick, S. E. and Hijmans, R. J. 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. – *Int. J. Climatol.* 37: 4302–4315.
- Filippelli, S. K., Falkowski, M. J., Hudak, A. T., Fekety, P. A., Vogeler, J. C., Khalyani, A. H., Rau, B. M. and Strand, E. K. 2020. Monitoring pinyon-juniper cover and aboveground biomass across the Great Basin. – *Environ. Res. Lett.* 15: 025004.
- Forest Inventory and Analysis. 2007. The forest inventory and analysis database: database description and users forest inventory and analysis program, vol. 3.– US Forest Service.
- Fricke, E. C., Ordonez, A., Rogers, H. S. and Svenning, J. C. 2022. The effects of defaunation on plants' capacity to track climate change. – *Science* 375: 210–214.
- García, C., Moracho, E., Díaz-Delgado, R. and Jordano, P. 2014. Long-term expansion of juniper populations in managed landscapes: patterns in space and time. – *J. Ecol.* 102: 1562–1571.
- Gehrt, S. D. and Brown, J. L. 2011. Is the urban coyote a misanthropic synanthrope? The case from Chicago. – *Cities Environ.* 4: article 3.
- Gibson, J., Moisen, G., Frescino, T. and Edwards, T. C. 2014. Using publicly available forest inventory data in climate-based models of tree species distribution: examining effects of true versus altered location coordinates. – *Ecosystems* 17: 43–53.
- Gifford, S. J., Gese, E. M. and Parmenter, R. R. 2017. Space use and social ecology of coyotes (*Canis latrans*) in a high-elevation ecosystem: relative stability in a changing environment. – *J. Ethol.* 35: 37–49.
- 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.
- González-Varo, J. P., Rumeu, B., Albrecht, J., Arroyo, J. M., Bueno, R. S., Burgos, T., da Silva, L. P., Escribano-Ávila, G., Farwig, N., García, D., Heleno, R. H., Illera, J. C., Jordano, P., Kurek, P., Simmons, B. I., Virgós, E., Sutherland, W. J. and Traveset, A. 2021. Limited potential for bird migration to disperse plants to cooler latitudes. – *Nature* 595: 75–79.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. – *Biol. Rev.* 52: 107–145.
- Grubbs, S. E. and Krausman, P. R. 2009. Use of urban landscape by coyotes. – *Southwest. Nat.* 54: 1–12.
- Guida, R. J., Abella, S. R., Roberts, C. L., Norman, C. M. and Smith, W. J. 2019. Assessing historical and future habitat models for four conservation-priority Mojave Desert species. – *J. Biogeogr.* 46: 2081–2097.
- Hernandez, P. A., Graham, C. H., Master, L. L. and Albert, D. L. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. – *Ecography* 29: 773–785.
- Herrera, J. M. and García, D. 2010. Effects of forest fragmentation on seed dispersal and seedling establishment in ornithochorous trees. – *Conserv. Biol.* 24: 1089–1098.
- Higginbotham, J. W. 1993. Rare plants: genetics and conservation. – *Ecology* 74: 2172–2173.
- Hody, J. W. and Kays, R. 2018. Mapping the expansion of coyotes (*Canis latrans*) across North and Central America. – *ZooKeys* 759: 81–97.
- Hohnung-Gaese, K. 2007. Do seed dispersers matter? A biogeographical approach. – In: Dennis, A. J., Schupp, E. W., Green, R. J. and Westcott, D. A. (eds), *Seed dispersal: theory and its application in a changing world* 2, 1st edn. CABI Publishing, pp. 545–560.
- Holthuijzen, A. M. A. and Adkisson, C. S. 1984. Passage rate, energetics, and utilization efficiency of the cedar waxwing. – *Wilson Bull.* 96: 680–684.
- Holthuijzen, A. M. A. and Sharik, T. L. 1985. The avian seed dispersal system of eastern red cedar (*Juniperus virginiana*). – *Can. J. Bot.* 63: 1508–1515.
- Homer, C. G., Dewitz, J. A., Yang, L., Jin, S., Danielson, P., Xian, G., Coulston, J., Herold, N. D., Wickham, J. D. and Megown, K. 2015. Completion of the 2011 National land cover database for the conterminous United States-representing a decade of land cover change information. – *Photogramm. Eng. Remote Sens.* 81: 345–354.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. – *Am. Nat.* 104: 501–528.
- Jensen, A. J., Marneweck, C. J., Kilgo, J. C. and Jachowski, D. S. 2022. Coyote diet in North America: geographic and ecological patterns during range expansion. – *Mamm. Rev.* 52: 480–496.
- Kitchen, A. M., Gese, E. M. and Schauster, E. R. 2000. Changes in coyote activity patterns due to reduced exposure to human persecution. – *Can. J. Zool.* 78: 853–857.
- Kremer, A., Ronce, O., Robledo-Arnuncio, J. J., Guillaume, F., Bohrer, G., Nathan, R., Bridle, J. R., Gomulkiewicz, R., Klein, E. K., Ritland, K., Kuparinen, A., Gerber, S. and Schueler, S. 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. – *Ecol. Lett.* 15: 378–392.
- Larson, R. N., Brown, J. L., Karels, T. and Riley, S. P. D. 2020. Effects of urbanization on resource use and individual specializations of coyotes. – *Landsc. Ecol.* 35: 111–125.

- zation in coyotes (*Canis latrans*) in southern California. – PLoS One 15: e0228881.
- Lendrum, P. E. 2017. Opportunistic foraging behavior by coyotes (*Canis latrans*) of a novel food source observed with remote cameras. – Southwest. Nat. 62: 308–311.
- Lenoir, J. and Svenning, J.-C. 2015. Climate-related range shifts – a global multidimensional synthesis and new research directions. – Ecography 38: 15–28.
- Levin, S. A., Muller-Landau, H. C., Nathan, R. and Chave, J. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. – Annu. Rev. Ecol. Evol. Syst. 34: 575–604.
- Levine, J. M. and Murrell, D. J. 2003. The community-level consequences of seed dispersal patterns. – Annu. Rev. Ecol. Evol. Syst. 34: 549–574.
- Longland, W. S. and Dimitri, L. A. 2016. Are western juniper seeds dispersed through diplochory? – Northwest. Sci. 90: 235–244.
- Martin, A. C. 1951. – In: Zim, H. S. (ed.), American wildlife and plants, a guide to wildlife food habits; the use of trees, shrubs, weeds, and herbs by birds and mammals of the United States. – McGraw-Hill Book Company.
- McKinley, D. C. and Blair, J. M. 2008. Woody plant encroachment by *Juniperus virginiana* in a mesic native grassland promotes rapid carbon and nitrogen accrual. – Ecosystems 11: 454–468.
- Merow, C., Smith, M. J. and Silander, J. A. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. – Ecography 36: 1058–1069.
- Norris, M. D., Blair, J. M. and Johnson, L. C. 2001. Land cover change in eastern Kansas: litter dynamics of closed-canopy eastern redcedar forests in tallgrass prairie. – Can. J. Bot. 79: 214–222.
- Osuri, A. M., Ratnam, J., Varma, V., Alvarez-Loayza, P., Hurtado Astaiza, J., Bradford, M., Fletcher, C., Ndoundou-Hockemba, M., Jansen, P. A., Kenfack, D., Marshall, A. R., Ramesh, B. R., Rovero, F. and Sankaran, M. 2016. Contrasting effects of defaunation on aboveground carbon storage across the global tropics. – Nat. Commun. 7: 11351.
- Pedrosa, F., Bercê, W., Levi, T., Pires, M. and Galetti, M. 2019. Seed dispersal effectiveness by a large-bodied invasive species in defaunated landscapes. – Biotropica 51: 862–873.
- Peres, C. A., Emilio, T., Schietti, J., Desmoulière, S. J. M. and Levi, T. 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. – Proc. Natl Acad. Sci. USA 113: 892–897.
- Phillips, S. J., Dudík, M. and Schapire, R. E. 2004. A maximum entropy approach to species distribution modeling. – Proc. 21st Int. Conf. on machine learning, ICML 2004, pp. 655–662.
- Phillips, S. J., Anderson, R. P., Dudík, M., Schapire, R. E. and Blair, M. E. 2017. Opening the black box: an open-source release of Maxent. – Ecography 40: 887–893.
- Ratajczak, Z., Nippert, J. B. and Collins, S. L. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. – Ecology 93: 697–703.
- Rau, B. M., Tausch, R., Reiner, A., Johnson, D. W., Chambers, J. C. and Blank, R. R. 2012. Developing a model framework for predicting effects of woody expansion and fire on ecosystem carbon and nitrogen in a pinyon-juniper woodland. – J. Arid Environ. 76: 97–104. <https://doi.org/10.1016/j.jaridenv.2011.06.005>
- Risson, A. 2012. The genetics of dispersal. – In: Cleobert, J., Baguette, M., Benton, T. G., Bullock, J. M. and Duceat, S. (eds), Dispersal ecology and evolution. Oxford Univ. Press, pp. 63–114.
- 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.
- Rogers, H. S., Beckman, N. G., Hartig, F., Johnson, J. S., Pufal, G., Shea, K., Zurell, D., Bullock, J. M., Cantrell, R. S., Loiselle, B., Pejchar, L., Razafindratsima, O. H., Sandor, M. E., Schupp, E. W., Strickland, W. C. and Zambrano, J. 2019. The total dispersal kernel: a review and future directions. – AoB Plants 11: plz042.
- Rogers, H. S., Donoso, I., Traveset, A. and Fricke, E. C. 2021. Cascading impacts of seed disperser loss on plant communities and ecosystems. – Annu. Rev. Ecol. Evol. Syst. 52: 641–666. <https://doi.org/10.1146/annurev-ecolsys-012221-111742>
- 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.
- Rowland, M. M., Suring, L. H., Tausch, R. J., Wisdom, M. J., Mary, M., Lowell, H., Robin, J. and Dynamics, M. J. 2011. Dynamics of western juniper woodland expansion into sagebrush communities in central Oregon. – Communities 1: 16.
- Rubalcava-Castillo, F. A., Sosa-Ramírez, J., Luna-Ruiz, 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.
- Sankey, T. T., Glenn, N., Ehinger, S., Boehm, A. and Hardegree, S. 2010. Characterizing western juniper expansion via a fusion of landsat 5 thematic mapper and lidar data. – Soc. Range Manage. 63: 514.
- Sauer, J. R., Hines, J. E., Fallon, J. E., Pardieck, K. L., Ziolkowski, D. J. Jr. and Link, W. A. 2014. The North American breeding bird survey, results and analysis 1966–2012, ver. 2. – Center, USGS Patuxent Wildlife Research.
- Schupp, E. W., Gómez, J. M., Jiménez, J. E. and Fuentes, M. 1997. Dispersal of *Juniperus occidentalis* (western juniper) seeds by frugivorous mammals on juniper mountain, southeastern Oregon. – Gr. Basin Nat. 57: 74–78.
- Schupp, E. W., Jordano, P. and Gómez, J. M. 2010. Seed dispersal effectiveness revisited: a conceptual review. – New Phytol. 188: 333–353.
- 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.
- Stiles, E. W. 2000. Animals as seed dispersers. – In: Fenner, M. (ed.), Seeds: the ecology of regeneration in plant communities, 2nd edn. CABI Publishing, pp. 111–124.
- Stricklan, D., Saud, P., Cibils, A. F., Steiner, R. L., Cram, D. S., Young, K. and Faist, A. M. 2020. Germination of one-seed juniper seeds distributed by different frugivore groups. – Rangel. Ecol. Manage. 73: 433–440.
- Suárez-Estebar, 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.
- Swart, N. C. et al. 2019. The Canadian Earth system model ver. 5 (CanESM5.0.3). – Geosci. Model Dev. 12: 4823–4873.
- Throop, H. L. and Lajtha, K. 2018. Spatial and temporal changes in ecosystem carbon pools following juniper encroachment and removal. – Biogeochemistry 140: 373–388.
- Traveset, A., Robertson, A. W. and Rodríguez-Pérez, J. 2007. A review on the role of endozoochory in seed germination. – In: Dennis, A. J., Green, R. J., Schupp, E. W. and Westcott, D. A. (eds), Seed dispersal: theory and its application in a changing world. CABI Publishing, pp. 78–103.

- USDA and NRCS 2020. The PLANTS database. – National Plant Data Team, <https://plants.sc.egov.usda.gov/home>.
- Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J. J. and Elith, J. 2022. Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. – *Ecol. Monogr.* 92: e01486.
- Van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. – *J. Environ. Manage.* 90: 2931–2942.
- Volder, A., Briske, D. D. and Tjoelker, M. G. 2013. Climate warming and precipitation redistribution modify tree-grass interactions and tree species establishment in a warm-temperate savanna. – *Global Change Biol.* 19: 843–857.
- Willson, M. F. 1993. Mammals as seed dispersal mutualist in North America. – *Oikos* 67: 159–176.
- Young, J. K., Andelt, W. F., Terletzky, P. A. and Shivik, J. A. 2006. A comparison of coyote ecology after 25 years: 1978 versus 2003. – *Can. J. Zool.* 84: 573–582.