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RESEARCH ARTICLE

Socio-ecological interactions promote outbreaks of a harmful invasive plant in an urban landscape

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Abstract

1. Urban landscapes often harbour organisms that harm people and threaten native biodiversity. These landscapes are characterized by differences in socioeconomic context, habitat suitability and patch connectedness. Identifying which spatial differences enable outbreaks of pests, pathogens and invasive species will improve targeted control efforts.
2. We tested hypotheses to explain the distribution and demography of puncturevine *Tribulus terrestris*, a human-dispersed invasive plant in Boise, a city in the western United States. We hypothesized an increase in puncturevine infestations near low-valued properties with a high proportion of bare ground, the species' preferred microhabitat, that are well connected on the urban road network. To test these hypotheses, we collected data on the abundance, emergence and persistence of reproductive plants in transects spanning >100 km of our study city. We then used hierarchical Bayesian models to evaluate the impacts of spatial covariates on puncturevine distribution and demography.
3. Bare ground cover consistently increased abundance, emergence and persistence of puncturevine, indicating the overarching importance of suitable establishment sites for this invasive species.
4. Property value had the strongest impact on puncturevine abundance and was the most important main effect in the model for puncturevine emergence. In both models, lower-valued properties had a higher risk of puncturevine occurrence.
5. The effects of road network connectivity depended on bare ground cover, with the highest predicted abundance and emergence of puncturevine in patches with low connectivity on the road network and high bare ground cover. Understanding these relationships will require data that can disentangle seed dispersal from establishment limitations.

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6. Identifying characteristics of urban patches that promote outbreaks of harmful species will improve the effectiveness and equity of control efforts. The prevalence of puncturevine in lower-valued properties is cause for concern as the plant impedes bicycle transportation, with the potential for disproportionate impacts on marginalized groups that lack resources to repair punctured tires. Our results add to a growing recognition that low-connectivity street networks have undesirable outcomes for environmental sustainability. As urban land cover continues to grow worldwide, accounting for interactions between human, natural and built systems will play a crucial role in managing invasive species.

KEYWORDS
active transportation, human-mediated dispersal, invasive species, network centrality, road network, spatial demography, urban ecology, wealth inequality

1 | INTRODUCTION

Urban land area, and the proportion of people that live in cities, is rapidly increasing (Liu et al., 2020; Zhou et al., 2019). The natural dynamics of urban ecosystems are crucial for human well-being and environmental sustainability. However, understanding urban ecosystems is complicated by unique interactions between human behaviour, the built environment and population dynamics of non-human organisms. Pest and pathogen outbreaks exemplify a population dynamic that is altered by socio-ecological interactions in cities. Human movement in urban transportation networks can increase rates of disease spread (Hackl & Dubernet, 2019) and extend dispersal distances for invasive species (von der Lippe et al., 2013). Patchy microhabitats that support pest and pathogen populations are also typical of urban environments, including breeding sites for insect disease vectors (Arunachalam et al., 2010) and soil seed banks for weedy plants (Figueroa et al., 2020). The distribution of microhabitats within cities is strongly influenced by social inequality (Schell et al., 2020), often resulting in a higher density of pest and pathogen species in marginalized communities (Des Roches et al., 2021). In other cases, households with higher income may manage for lower biodiversity (e.g. monoculture lawns—Blanchette et al., 2021). All three urban factors—human movement, microhabitat availability and socioeconomic variability—interact across scales to determine the spread of harmful organisms (Niemiec et al., 2018).

Spatial heterogeneity in cities challenges our ability to predict organismal spread but also provides opportunities for targeted control. Planned efforts to prioritize patches for management efforts can aid disease eradication (Ruktanonchai et al., 2016) and slow invasive species spread (Perry et al., 2017). Equitable resource allocation across socioeconomically variable neighbourhoods can alleviate biases in where pest and pathogen control efforts take place (Sánchez et al., 2021). Relative to unplanned efforts, targeted control can reduce costs and improve outcomes (Ashander et al., 2021; Potgieter et al., 2022). Achieving the benefits of targeted control will require geospatial analyses to identify which patches are likely to contribute most to organismal spread.

Differences in the potential for spread are a major determinant of how individual patches contribute to landscape spread. Spatial networks, with edges representing dispersal pathways and nodes representing potential habitat patches, are often used to model the spread of invasive species and pathogens (Chadès et al., 2011). Whether invading species are introduced at central or peripheral patches within spatial networks can determine subsequent rates of landscape spread (Minor & Gardner, 2010). In turn, targeting removal efforts to highly connected patches is often an effective strategy for reducing spread (Perry et al., 2017). For species with human-mediated dispersal, transportation infrastructure generates the template for dispersal networks (Bullock et al., 2018). Spatial data on transportation infrastructure (i.e. roads) thus present novel opportunities to detect (Cook et al., 2019) and control invasive species (Hulme, 2009). One assumption of using network-based metrics to represent invasion potential is that dispersal between patches is the most important barrier to spread. However, patches can also vary in suitability for local population growth, particularly in heterogeneous urban environments.

Patches, where populations can achieve sufficient reproductive success to produce individuals that spread to other patches, represent demographic sources that are particularly important for outbreaks of pests and pathogen species (Ruktanonchai et al., 2016). In contrast, demographic sinks are patches where the mortality of individuals prevails over reproductive success, and populations are maintained by immigration from other habitats (Pulliam, 1988). In cities, barriers to establishment create demographic sinks that can limit population growth rates (Piana et al., 2019). Urban microhabitats that enable reproductive success, from standing water to bare ground, are often embedded in a matrix of unsuitable habitats (e.g. impervious surfaces; Cheptou et al., 2008). Identifying which microhabitats act as demographic sources and which act as demographic sinks is a crucial step for targeted control, as focusing efforts on source patches increases the likelihood of eradication (Ruktanonchai et al., 2016).

Socioeconomic context can determine whether patches are sources or sinks for invasive species. Accounting for socioeconomic context, including land tenure, human population density, housing age and family income, often improves spatial models for invasive species distribution (Gulezian & Nyberg, 2010; Jang et al., 2020; Niemiec et al., 2018). Understanding why invasive species prevalence correlates with socioeconomic factors can inform control techniques, for example, whether preventative or transformative management strategies are more likely to limit invasion (Niemiec et al., 2020). From an equity perspective, socioeconomic data can identify management disparities between privileged and marginalized communities (Schell et al., 2020). Time series of invasive species occurrence are currently uncommon, relative to data on static distributions, but will improve our capacity to disentangle socio-ecological factors that drive invasion patterns (Niemiec et al., 2020). More broadly, studies that evaluate socioeconomic context as a component of spatial demography, including source-sink dynamics, will be essential to understand how invasive plants spread in urban landscapes.

In this study, we model the abundance and temporal dynamics of an invasive plant that colonizes urban transportation networks. The focal species is puncturevine *Tribulus terrestris*, an invasive plant species, considered a noxious weed throughout western North America (Harrington & Reichard, 2007). Puncturevine seeds are human-dispersed by spiny fruits that embed themselves in bicycle tires, shoes and other moving objects (Johnson et al., 2020). This dispersal strategy means that puncturevine receives direct benefits from harming humans, broadly analogous to many other pests and pathogens. Stakeholders in our study city have identified puncturevine eradication as a top priority, as the plant impedes bicycle travel. Our objective was to apply spatial data on transportation networks, socioeconomic conditions and microhabitat availability to identify patches in the city likely to contribute to puncturevine outbreaks. To accomplish this goal, we collected data on puncturevine distribution and demography in city-wide transects spanning >100 km. We hypothesized the following:

1. Higher road network connectivity increases the abundance and emergence of reproductive plants;
2. Prevalence of suitable microhabitats for establishment increases abundance and emergence of reproductive plants;
3. Lower property value increases the abundance and persistence of puncturevine, as wealthier areas have more resources for invasive plant removal.

2 | MATERIALS AND METHODS

2.1 | Study site

Our study took place in Boise, Idaho (43°37′12.0″N, 16°13′12.0″W). Boise's climate is hot and dry from June to September, where the average daily temperature is >28°C, and cold from October to May, with temperatures that frequently drop below 0°C. Annual precipitation is 31.39 cm, the majority falling in the cold season. The city of Boise was established in the 1860s and is now one of the fastest growing cities in the United States, including a rapid increase in urban land cover (Narducci et al., 2019). Our study area represents 231 km^2 within the city limits of Boise, for a total population of 248,000 people.

2.2 | Study species

Puncturevine (*Tribulus terrestris* L.) is native to Southern Europe but has spread to arid climates worldwide (El-Ghareeb, 1991). The first recorded instance of puncturevine plants in Boise was in 1972 (Ertter 9455 CIC). In cold climates, such as Idaho, puncturevine grows as an annual, with seeds that can remain dormant in the seed bank for at least 3–6 years (Ernst & Tolsma, 1988). The plant produces schizocarps (dry fruits or nutlets), each consisting of five mericarps, with two woody spines per mericarp. In Boise, bicycle tire punctures from these woody spines are a serious problem, resulting in mass city-wide efforts to eradicate puncturevine. These efforts culminate in an annual festival (named after the vernacular word for puncturevine, goathead—'Goathead fest') that celebrates the removal of several thousand kilograms of puncturevine plants by volunteer teams. Outside of Boise, puncturevine has regional importance as an invasive plant with high priority for control across western North America (DiTomaso et al., 2013; Harrington & Reichard, 2007).

2.3 | Sampling scheme

We sampled puncturevine plants using two separate schemes: single-survey plots where abundance was measured once per plot and repeat-survey plots where presence-absence was measured multiple times during the growing season (Figure 1). These complementary sampling schemes enabled us to estimate whole-city patterns of abundance across a large number of plots (single survey) as well as temporal patterns of emergence and persistence across a smaller number of repeat plots (repeat survey). Both single- and repeat-survey plots were nested within transects corresponding to segments of Boise's transportation network.

To initiate single-survey plots, we generated a layer of randomly selected points within Boise city limits, with a minimum distance of 350 m between points. In the field, we navigated to the street intersection nearest to the randomly selected point and began transects at that point. Single-survey plots were generated by splitting transects into smaller subunits (plots). Our goal was for transects to span a city block (i.e. a rectangular area surrounded by roads) beginning and ending at the random starting point. For some random sampling points, walking in a square route was impossible, and we walked transects that approximated 300 m (the typical length of a city block). Transects included both sides of the road within each route. We recorded transect paths using a GPS

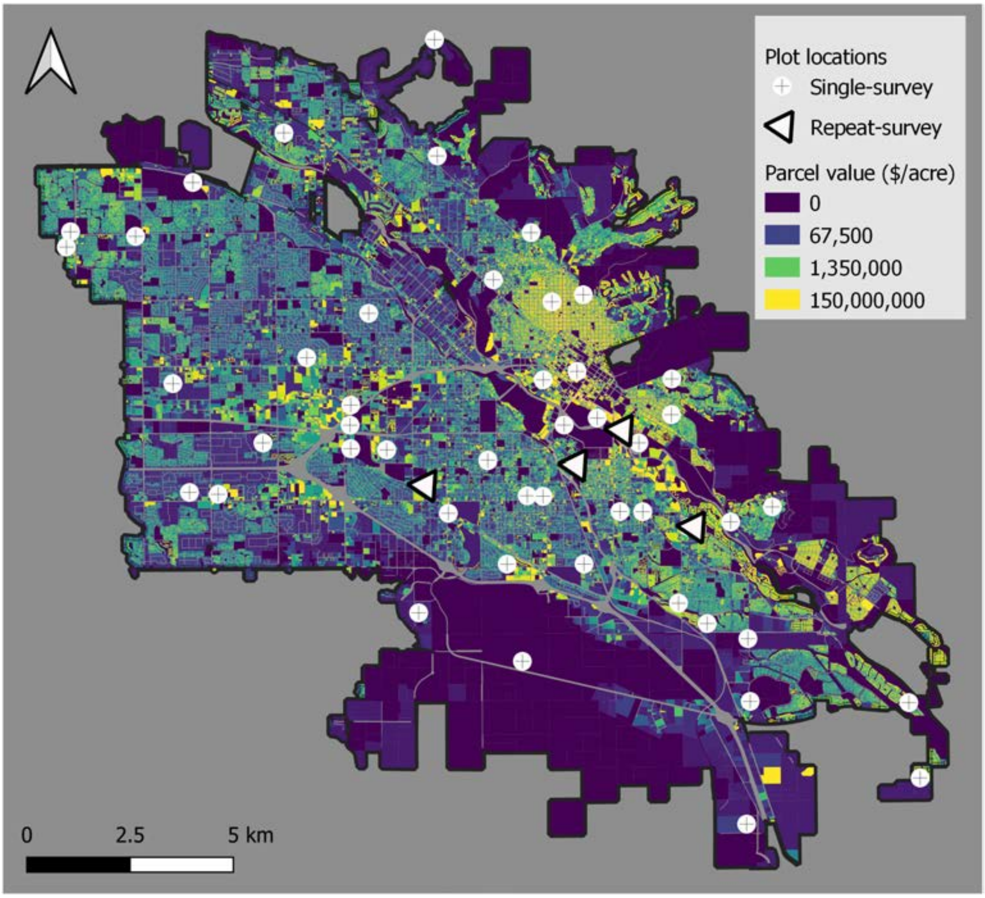

FIGURE 1 Location of sampling units across gradients of property value in Boise, Idaho, United States.

receiver (Bad Elf GNSS Surveyor, accuracy <1 m). On the date that a transect was surveyed, we recorded the coordinates of every reproductive puncturevine plant with visible flowers or fruits within 0.5 m of the boundary between paved and unpaved ground. The 0.5 m buffer on either side of the transect was selected as a distance that was short enough to enable visual surveys of puncturevine plants without walking off the transect pathway. Single-survey sampling began several weeks after puncturevine plants in the city started to flower until the onset of cooler temperatures, from 13 July to 22 September 2020.

We used a similar spatial design for repeat-survey plots, including transect paths along paved routes, with plants recorded within 0.5 m of the walked route. To facilitate repeat sampling, repeat-survey transects were opportunistically located. Locations of both repeat- and single-survey plots were determined independent of land use. Each repeat-survey transect covered various urban environmental and socioeconomic contexts, including multiple city blocks. Data recorders walked repeat-survey transects weekly from 22 May to 17 October 2020, a period of 21 weekly intervals. During each repeat survey, walkers recorded puncturevine presence in spatial units of 2 × 0.5 m. These spatial units represent rectangles on either side of a transect, with the 0.5 m distance perpendicular to the transect and the 2 m distance parallel to the transect. All transects were located on public thoroughfares and sampling did not require field permits.

2.4 | GIS processing

We processed GPS-recorded transect paths and puncturevine points to generate spatial data on puncturevine abundance (single-survey plots) and presence-absence (repeat-survey plots). We applied a 0.5 m buffer to transect lines to match the area searched for puncturevine plants. This operation resulted in transect polygons with a width of 1 m. We clipped these transect polygons into segments using cadastral data on property boundaries acquired from the Ada County Assessor's Office, with each resultant segment identified to the nearest property. We further subdivided segments into ~5 m^2 plots (mean ± SD: 5.02 ± 1.1 m^2) using the Voronoi Polygons algorithm in QGIS (v. 3.14.1 Pi; QGIS Development Team, 2021). We selected 5 m as the length of our plots to ensure that at least three plots were represented within residential properties, which have a typical street-facing border length of ~20 m. For a visual illustration of workflows used to construct abundance, emergence and persistence data see Figure S1.

For single-survey plots, we matched puncturevine GPS points to the nearest ~5 m^2 plot and counted the number of records within each plot to represent abundance. We considered GPS points >10 m away from any plot as errors and discarded them. Single-survey plots with no matching puncturevine GPS points were recorded as having zero reproductive puncturevine plants.

After processing, single-survey plot data included 48 transects, with a total transect length of 78.73 km and 12,810 single-survey plots (Figure S1).

For repeat-survey plots, we recorded puncturevine as present if a plot sampled at a given week matched with at least one puncturevine GPS point. To process presence-absence data for analysis, we created two separate datasets: (1) Emergence data, only including plots that began a weekly time interval with puncturevine absent. Transitions from absence to presence of reproductive plants were considered a successful emergence event. (2) Persistence data, only including plots that began a weekly time interval with puncturevine, were present. The continued presence of reproductive plants was then considered successful persistence. Individual plots could be included multiple times in both emergence and persistence datasets, as some plots transitioned from absence to presence (and vice versa) multiple times during the study. Repeat-survey plots included four transects for a total length of 25.13 km. The sample size for the emergence and persistence datasets depended upon the absence or presence of puncturevine in previous timesteps, ultimately resulting in 5029 unique plots for emergence and 323 unique plots for persistence (Figure S1). All plot data are publicly available from Caughlin et al. (2023).

2.5 | Spatial covariates

To test hypotheses, we developed three spatial covariates: property value, betweenness (a measure of network connectivity) and bare ground cover. We then matched spatial covariates to the nearest plot in the single-survey abundance and repeat-survey emergence and persistence datasets. Processing spatial covariates for use in statistical models necessarily involves choices on appropriate spatial extent and resolution to match covariates with a response variable (in this case, geolocated puncturevine plants). As our primary objective for this study was to test hypotheses rather than explore data or make predictions (Tredennick et al., 2021), we aimed to minimize model selection by making a priori choices on how to process covariates for our models. We based these choices on previous literature and our biological knowledge of the study system, and when possible, chose the simplest representation of each covariate.

Property value was extracted from cadastral data provided by the Ada County Assessor's office, which uses mass appraisal techniques to estimate the value of every property in the county. To account for parcels with different areas, we divided property value by the total acres of the parcel. To spatially match property value to puncturevine plots, we assigned each plot a property value based on the distance from a plot to the parcel boundary. We excluded plots with a distance to the nearest parcel boundary >20 m. This approach assumes that management efforts differ between puncturevine plots based on proximity to high versus low-valued properties. For example, we expect a puncturevine plot in a public pathway near a high-valued property to receive more invasive plant control than a puncturevine plot in a public pathway near a low-valued property.

To account for how central each puncturevine plot was on Boise's transportation network, including roads open to vehicle traffic and pathways limited to bicycle and pedestrian traffic, we calculated betweenness centrality across the city's road network. We selected betweenness to represent connectivity in our study as previous studies have shown that higher betweenness centrality enables faster spread of invasive species throughout networks (Ashander et al., 2021; Minor & Gardner, 2010; Perry et al., 2017). Betweenness centrality represents the number of shortest network paths connecting each unique combination of nodes. Nodes with high betweenness centrality are expected to have the greatest amount of flow through the network; in this case, street traffic (Kirkley et al., 2018). We calculated betweenness centrality for ~10 m length road segments using a GIS layer developed by the City of Boise in 2016 that included both roads and bicycle and pedestrian-only paths. Our results were robust to different processing choices for road segment length. Next, we applied a betweenness algorithm using the R package 'IGRAPH', to calculate the betweenness centrality for each segment v in the road network (Csardi & Nepusz, 2006). This algorithm sums the number of shortest paths between every unique combination of segments j and i which pass through segment v, where $j \neq i \neq v$. Finally, we assigned each puncturevine plot the betweenness value of the nearest road segment, discarding plots >10 m from any road segment.

To represent the abundance of suitable microhabitats for puncturevine, we determined the area of bare ground cover around each plot. Previous studies have identified this land cover class as a preferred establishment site for the species (El-Ghareeb, 1991). Examples of bare ground in our study area include vacant lots, brown space on the side of canals and neglected patches of land near traffic corridors. We determined bare ground cover using 2019 imagery with 1 m resolution from the U.S. Department of Agriculture's National Agriculture Imagery Program (NAIP). This imagery was acquired in summer 2019 with complete coverage of the study area in four bands (red, green, blue and near-infrared). We then developed a land cover classification in Google Earth Engine. Our land cover classification began with object-oriented image analysis to segment spectrally-similar clusters of pixels. We developed a dataset of manually-classified objects ($N = 1800$) and used this dataset to train a random forest algorithm to identify land-cover types in imagery. The final classification had 87.58% and 73.70% user's and producer's accuracies for the bare ground class, respectively. We then calculated the summed area of bare ground cover within 30 m of each puncturevine plot for use in analyses.

2.6 | Statistical analysis

We analysed our data using generalized linear mixed-effect models (GLMMs). To facilitate the comparison of model outputs between our three datasets (abundance, emergence and persistence), we included the same set of three covariates across all models. Models included the main effects of property value, betweenness centrality and bare ground cover. Correlations between these predictor variables were minimal (Pearson's $r < 0.2$ in all cases). Because we anticipated that suitable establishment patches (represented by bare ground cover) would require seed arrival (represented by betweenness centrality) for puncturevine population growth, we also included an interaction term for betweenness centrality and bare ground cover. We centered covariates around the mean and divided them by two standard deviations to aid direct comparisons of relative effect size (Gelman, 2008).

To account for spatial non-independence, we modelled the membership of plots in transects as a random intercept. Transects correspond to approximately one city block. At a finer spatial scale, we also modelled the membership of plots in streets, using the name of the nearest street to each plot as a random intercept. These random effects represent our expectation that baseline puncturevine abundance depends on which transect and which street a plot is located in. Random effects were non-nested. In addition to street and transect effects, the emergence and persistence models included the week of sampling as a random intercept to account for temporal replication.

We modelled count data on puncturevine abundance in single-survey plots using a negative binomial distribution and binary data on puncturevine persistence and emergence in repeat-survey plots using a Bernoulli distribution. Because plot area could be somewhat variable due to the irregular shape of some streets, we accounted for variable plot size as an offset in our negative binomial GLMM (Hilbe, 2011) and as an exposure term in our Bernoulli models (Bolker, 2012). The negative binomial GLMM used a log-link to constrain predictions to the positive scale, and the Bernoulli GLMMs used a complementary log–log ('cloglog') link to constrain predictions to the probability scale.

GLMMs were fit in a hierarchical Bayesian framework with the Stan programming language accessed through the R package 'BRMS' (Bürkner, 2017). Posterior samples for each model were drawn using four chains with 2000 iterations, discarding the first 1000 as warmup. To improve model fit, including potential multicollinearity between our predictor variables, we modelled effect sizes using regularized horseshoe priors. Regularization 'shrinks' parameter estimates closer to zero, resulting in more conservative estimates for effect size (McElreath, 2020). We assessed model convergence using the R-hat and effective sample size statistics provided by the brms package, visually examining posterior predictions and trace plots of HMC chains and ensuring that there were no divergent transitions in HMC chains. We quantified model fit using a Bayesian version of R^2 (Gelman et al., 2019).

3 | RESULTS

3.1 | Data summary

Single-survey plots ($N=12{,}810$) included a total of 327 puncturevine plants, with a mean (±SD) density of 0.006 ± 0.108 plants m^{-1}. Repeat-survey plots included a total of 578 emergence events ($N=57{,}716$ weekly plot records) and 566 persistence events ($N=1104$ weekly plot records), resulting in a 0.010 probability of weekly emergence and a 0.558 probability of weekly persistence across all plots.

3.2 | Single-survey results

Property value had the strongest impact on puncturevine abundance in single-survey plots (Figures 2 and 3). An average plot with the minimum property value observed in the dataset was expected to have an additional 0.005 plants m^2 (95% CI: 0.002 to 0.145 plants) compared to a plot with the maximum property value.

Microsite availability, represented by bare ground cover, had a strong positive effect on puncturevine abundance. Comparing an average plot with zero bare ground to a plot with the maximum bare ground observed in the data, our model predicts a median increase in density of 0.013 plants m^2 (95% CI: 0.001 to 0.087 plants per m^2). In contrast to the positive effect of microsite availability, network connectedness (represented by street betweenness) negatively affected puncturevine abundance. Comparing an average plot with minimum betweenness to one with maximum betweenness, puncturevine density decreased by a median of 0.001 plants m^2 (95% CI: 0.004 to 0.00) in the plot with maximum betweenness.

We found strong evidence for an interaction between street betweenness and bare ground cover. The interaction term between the two variables was negative, with a median value of −4.63 (95% CI: −6.25 to −3.21). This negative term reveals that bare ground cover has a positive impact on puncturevine abundance at low levels of betweenness. However, as betweenness increases, the effect of bare ground cover switches from positive to negative. A spatial interpretation of these results is that opposite spatial contexts promote puncturevine abundance: areas with high bare ground but low betweenness *and* areas with low bare ground but high betweenness (Figure 4).

3.3 | Repeat-survey results

Statistical results for puncturevine emergence were similar to abundance, including a decreased probability of emergence with higher property value and an increased probability of emergence with higher bare ground (Figure 5). For an average plot with minimum property value, compared to an average plot with maximum property value, the probability of emergence decreased by 2.60% (95% CI: 0.00% to 26.1%). In contrast to models for abundance, bare ground had a much stronger impact than property value on the probability of emergence. When comparing an average plot with minimum bare ground cover to an average plot with the maximum bare ground cover, the probability of emergence increased by 21.7% (95% CI: 1.2% to 96.4%).

The effect of betweenness on puncturevine emergence was highly certain, including a probability that betweenness had a negative effect on the emergence of >98%. However, the effect size was near zero for this covariate. Despite relatively weak effects of

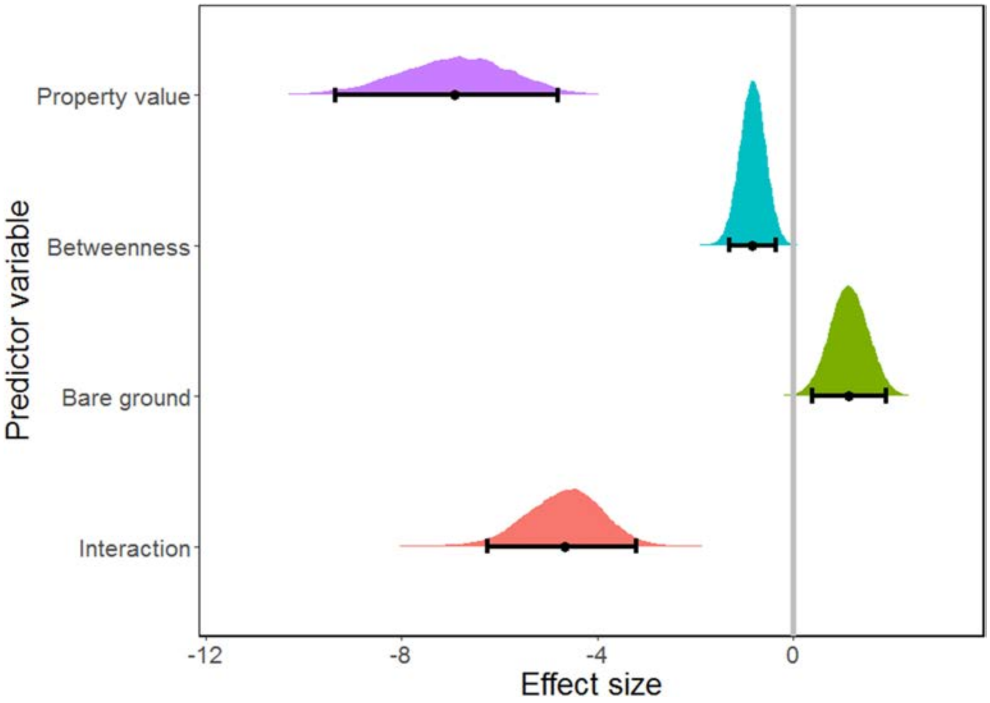

FIGURE 2 Posterior distributions for predictor variables from generalized linear mixed-effect model for puncturevine abundance measured in single-survey plots. The location of each posterior distribution relative to zero (indicated by a vertical line) indicates whether the predictor had a positive or negative impact on abundance. The interaction term refers to an interaction between street betweenness and bare ground. Wider posterior distributions indicate higher uncertainty. Dots and lines at the bottom of each posterior distribution indicate the median and 95% credible interval for each effect.

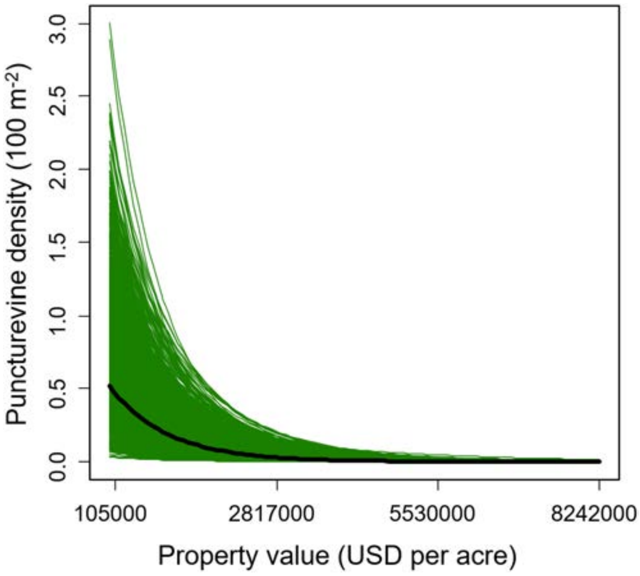

FIGURE 3 Predicted response of puncturevine density to property value. Predictions represent an average site with an area of 100 m^2 (a typical area of a sidewalk in front of an urban home in Boise). Thin green lines represent posterior predictions from the Bayesian generalized linear mixed-effect model for puncturevine abundance. All 4000 posterior draws are represented in the figure. The thick black line represents median predicted response.

betweenness as a main effect, the interaction term between betweenness and bare ground cover was the strongest effect in the emergence model. Similar to the abundance model, the interaction term was negative (median: −2.85 [95% CI: −3.75 to −1.99]). This negative term reveals the highest probability of emergence for plots with low betweenness and high bare ground as well as modest increases in the probability of emergence for plots with high betweenness and low bare ground (Figure 6).

In contrast to abundance and emergence models, we found weak and uncertain effects of all covariates in the model for puncturevine persistence (Figure S2). While all predictor variables for the abundance and emergence models had probabilities of direction >98%, indicating high certainty that an effect was either positive or negative, no predictor variable in the persistence model had a probability of direction >90%. The strongest effect in the persistence model was bare ground cover, with a positive impact, including a median effect of 0.26 (95% CI: −0.07 to 0.73). Other effects in the persistence model were centered around zero, suggesting no detectable impact on probability of puncturevine persistence.

3.4 | Model fit

Bayesian R^2 values varied between models. The persistence model had the highest median R^2, with 34.3% variance explained, albeit

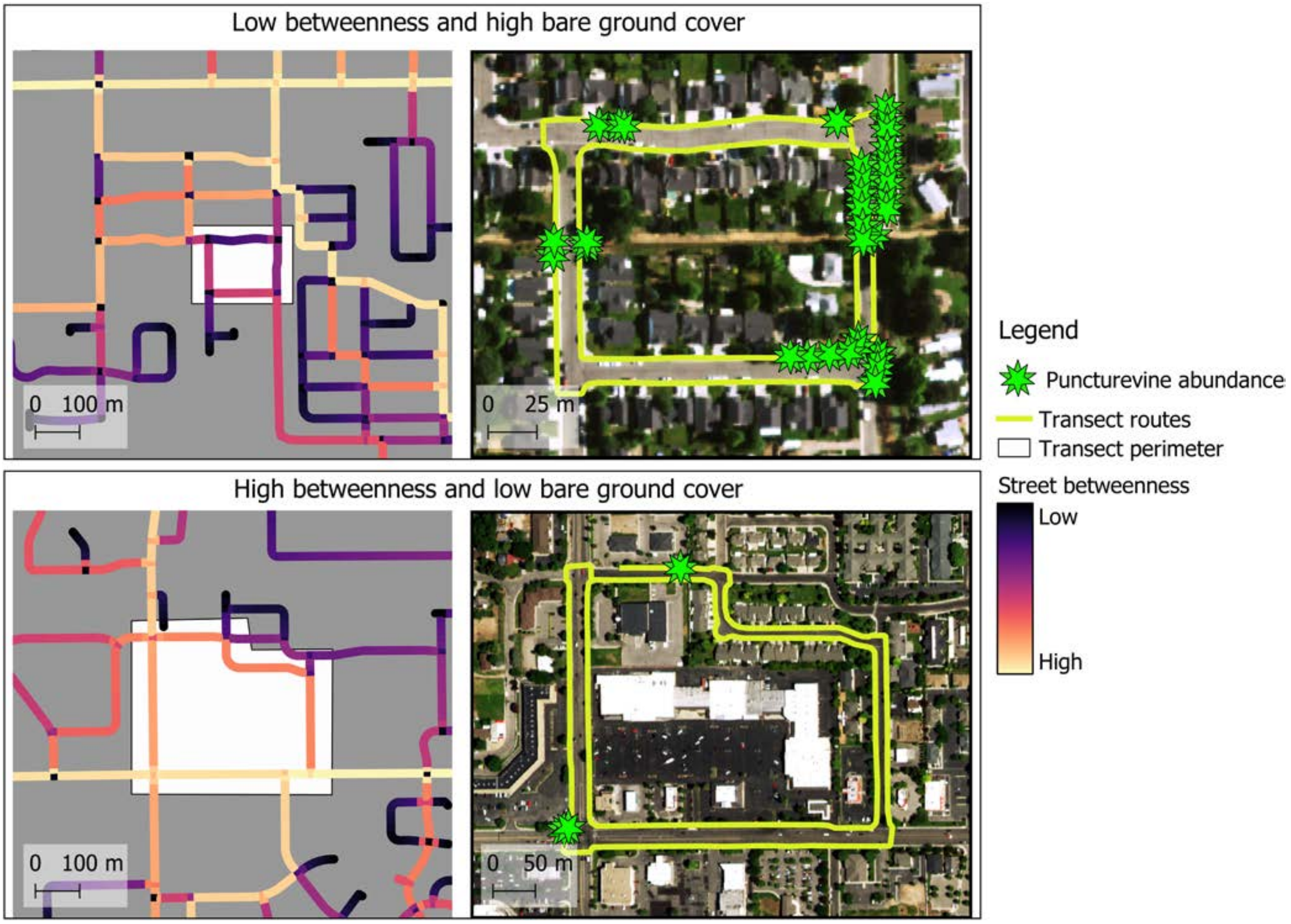

FIGURE 4 Puncturevine abundance is higher in sites with contrasting levels of network betweenness and bare ground cover. These maps illustrate the effect of the interaction term in Figure 2.

with high uncertainty (95% CI: 4.0% to 38.8%). In contrast, the emergence model had a median R^2 of 10.2% (95% CI: 2.0% to 12.9%), and the single-survey abundance model had a median R^2 of 23.6% (95% CI: 8.5% to 46.0%).

4 | DISCUSSION

We studied how three defining features of urban landscapes, microhabitat heterogeneity, street connectivity and economic inequality, shape the distribution of an invasive plant. All three of these features had strong impacts on abundance and emergence of reproductive plants. Patches vulnerable to puncturevine invasion had the following characteristics: bare ground near low-valued properties peripheral to the road network. These results illustrate how socioeconomic context and transportation infrastructure alter the suitability of microhabitat patches for puncturevine, an invasive plant species. We found that accounting for the complexity of the human environment was critical to understanding puncturevine's urban distribution. Fortunately, spatially extensive data on city road networks and property characteristics are widely available and well suited for incorporation into ecological models, such as our GLMMs for puncturevine distribution and demography. Like many other harmful organisms prevalent in cities, puncturevine degrades biodiversity and negatively impacts human well-being. Eradicating these organisms by targeting source patches will improve city life for people and native biota.

Our results show how the availability of suitable microhabitats limits puncturevine abundance. Bare ground cover consistently increased abundance, emergence and persistence of puncturevine. This finding highlights the role that microhabitat availability in urban environments can play in pest and pathogen outbreaks (Arunachalam et al., 2010). Identifying and eliminating microhabitats that facilitate establishment, such as patches of bare ground that enable puncturevine infestations, presents one option for control. These microhabitats not only create habitat for invasive species but also present opportunities for restoration if bare ground can be replaced with beneficial plant species (Aronson et al., 2017; Figueroa et al., 2020). Despite the overarching importance of bare ground cover for puncturevine distribution and demography, patches of bare ground vary in connectivity and socioeconomic context. Our study enabled us to quantify the relative importance of these contextual factors for puncturevine invasion.

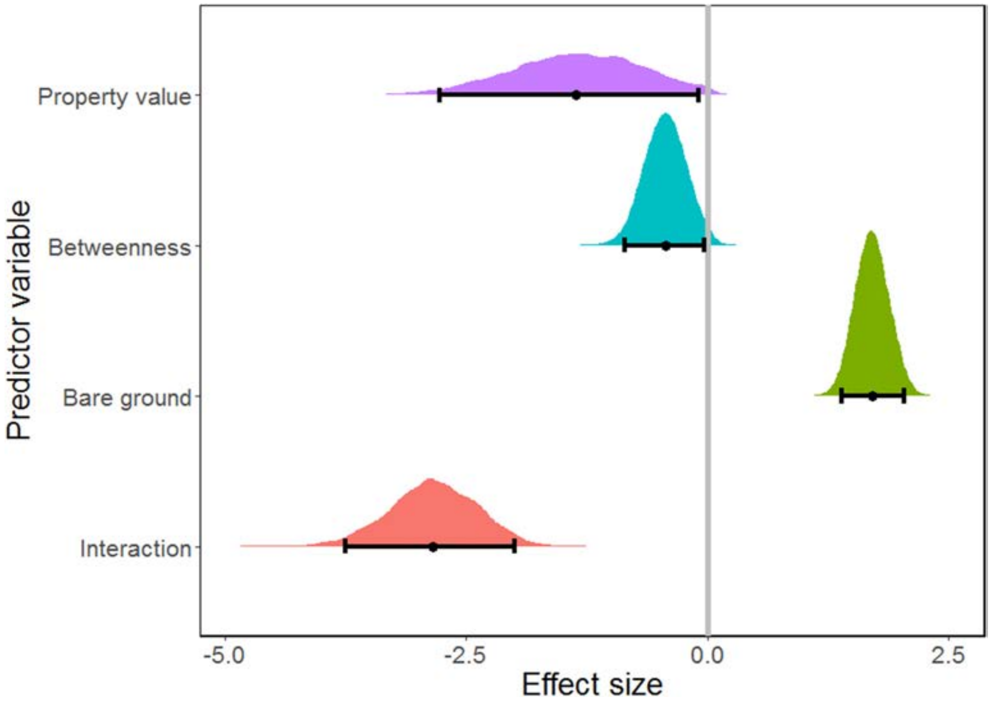

FIGURE 5 Posterior distributions for predictor variables from generalized linear mixed-effect model (GLMM) for puncturevine emergence measured in repeat-survey plots. The location of each posterior distribution relative to zero (indicated by a vertical line) indicates whether the predictor had a positive or negative impact on emergence. The interaction term refers to an interaction between street betweenness and bare ground. Wider posterior distributions indicate higher uncertainty. Dots and lines at the bottom of each posterior distribution indicate the median and 95% credible interval for each effect.

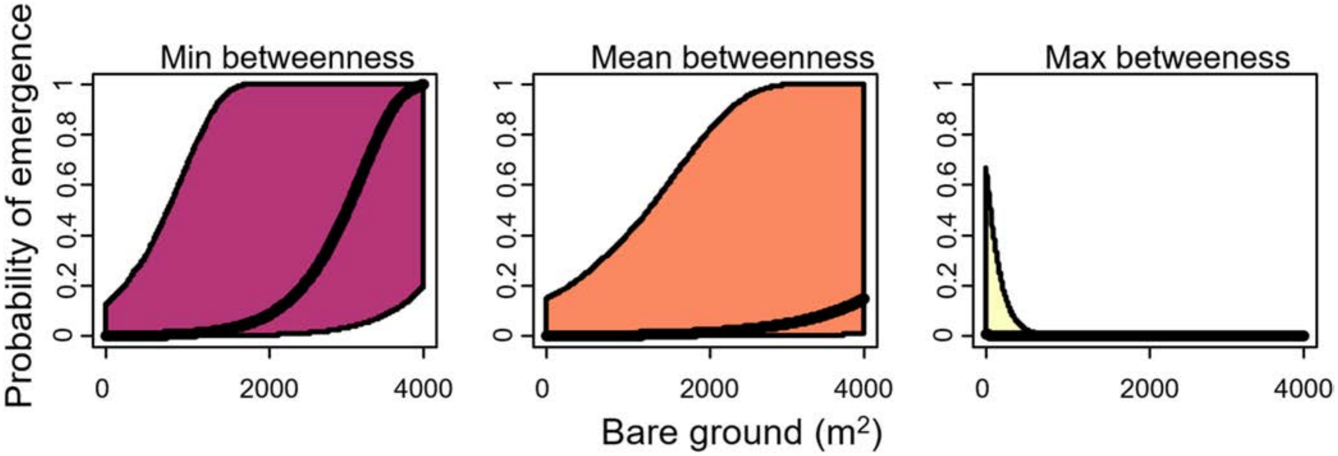

FIGURE 6 Impact of network betweenness and bare ground on puncturevine emergence. This figure illustrates the impact of the interaction term in Figure 5 on probability of puncturevine emergence, estimated from the generalized linear mixed-effect model. The thick black line indicates the mean response and shaded polygons represent 95% credibility intervals.

Property value was the single most important predictor of puncturevine abundance and the most important main effect in the puncturevine emergence model. Our work adds to a growing body of evidence that social inequality shapes ecological dynamics in urban environments, including a higher prevalence of harmful species in lower-income neighbourhoods (Des Roches et al., 2021; Schell et al., 2020). Puncturevine outbreaks may be less common in high-value properties if wealthier landowners have more time and financial resources for yard maintenance, including invasive plant removal and prevention of bare ground through more intensive landscaping and watering. Other species of invasive plants, such as Albizia trees with property-damaging limbs (Niemiec et al., 2018) and burdock plants with clinging fruits (Gulezian & Nyberg, 2010), also tend to have lower occurrence in high-income areas. In contrast, exotic species with perceived value, such as ornamental species, may have a higher prevalence in wealthier neighbourhoods (Ward

& Amatangelo, 2018). City-wide puncturevine removal efforts, currently led by volunteers, may also be more focused on higher-income areas, as volunteers tend to be from higher socioeconomic groups with free time to participate in civic activities (Merenlender et al., 2016). Testing for spatial biases in current removal efforts will require additional data, for example, surveying volunteers to identify where they tend to search for puncturevine. We also note that our study includes plots with a variety of land tenure, including residential properties, commercial land and public spaces, the latter often assessed with less value than other land types. While including these categories as variables did not improve model fit, more detailed cadastral data would likely provide additional explanatory power for puncturevine distribution (e.g. residence time in properties; Niemiec et al., 2018). Economic disparity where puncturevine outbreaks occur likely has detrimental consequences for marginalized communities that may rely more on bicycle travel for everyday commuting and have fewer resources to repair damaged tires (Lee et al., 2017).

Puncturevine populations that are overlooked in removal efforts, such as low-valued properties, could undermine eradication efforts as seeds from neglected patches re-colonize managed patches. We hypothesized centrally located patches would have greater abundance and puncturevine emergence due to increased seed arrival from human movement. Our results did not support this hypothesis. Instead, the effects of network connectivity ranged from positive to negative, depending on the availability of bare ground cover. Plots with high bare ground cover and low network betweenness were predicted to have higher puncturevine abundance and probability of emergence. This result implies that peripheral plots along the road network, such as cul-de-sacs, dead-end streets and gated communities, are at higher risk of puncturevine invasion as long as bare ground cover is present. One interpretation of this result is that our road network variable is correlated with characteristics of the urban environment unrelated to human-mediated seed dispersal. For example, poorly-connected areas of the road network may be overlooked in removal efforts. Alternately, seed dispersal by bicycle and pedestrian movements may be higher in peripheral areas if people prefer to move through these areas to avoid high vehicle traffic. Additional data, such as spatially-explicit data on human movement (Ruktanonchai et al., 2018) or experimental tests of human-mediated dispersal distances (Wichmann et al., 2009), will be required to disentangle these possibilities. Regardless of the causal pathways behind our results, network betweenness had consistent effects across independent models for emergence and abundance, reinforcing the value of network metrics for predicting invasive species distributions (Minor & Gardner, 2010; Perry et al., 2017). Furthermore, our finding that a harmful invasive species are more prevalent in poorly connected patches contributes to the growing list of environmental and health problems associated with sprawling and disconnected road networks (Barrington-Leigh & Millard-Ball, 2020).

Our study can guide the management of puncturevine in cities across western North America, where the invasive plant poses a regional threat to human well-being and native ecosystems (DiTomaso et al., 2013). We found that patches occupied by puncturevine plants were rare, including <2% of surveyed plots. Furthermore, the emergence of new plants is an infrequent event, with a weekly probability of emergence <0.01%. The apparent rarity of suitable patches for puncturevine points to the feasibility of spatial targeting for population control. We have demonstrated that socio-ecological variables can predict which patches are most likely to host puncturevine plants. Because these variables—bare ground cover, property value and street network connectivity—are spatially extensive, producing city-wide maps to guide management efforts is an achievable next step (e.g. Potgieter et al., 2022). Ongoing volunteer-led weeding efforts, such as Boise's Goathead Fest, could take advantage of maps of puncturevine hotspots to direct volunteers to areas that currently may be overlooked, including neighbourhoods with low property value. Given the relatively small number of suitable patches, cost-intensive preventative control measures such as eliminating bare ground by planting native species or soil removal to eradicate puncturevine seed banks could also be feasible management options. Although our study takes place in a single city, puncturevine prevalence and management efforts are broadly similar between Boise and other cities in western North America (e.g., https://www.slc.gov/parks/trails-natural-lands/puncturevinefree/), and we anticipate that our results have relevance for control across the region.

Understanding demographic bottlenecks that limit puncturevine spread will facilitate choosing between management options that vary in their impact across the plant life cycles (Reaser et al., 2008). We evaluated whether spatial covariates had different effects on emergence versus persistence of reproductive puncturevine and how potential differences related to overall abundance patterns. We found similar effects of property value, bare ground cover and network betweenness across both the emergence and abundance models, including an interaction between bare ground cover and network betweenness (Figures 2 and 5). Similar effect sizes between puncturevine abundance and emergence models, despite different sampling strategies and model structure, increase confidence that our covariates are related to puncturevine demography. In contrast, these effects were weak and uncertain in models for puncturevine persistence. As an annual species with rapid growth, recruitment processes related to emergence may have more influence on puncturevine's overall distribution than established plants' survival. Alternately, current puncturevine removal efforts are more likely to impact persistence than emergence, potentially weakening links between environmental covariates and persistence. Recruitment processes before the emergence of reproductive plants in our study include seed arrival, seed dormancy in the seed bank, germination and seedling establishment. We expect that recruitment limitation related to bare ground cover and property value impacts at least one of these demographic transitions, ultimately constraining overall puncturevine abundance. More detailed demographic data representing the full plant life cycle (see Piana et al., 2019) will be required to disentangle the role of seed and site limitation for puncturevine populations.

Boise, Idaho, exemplifies the future of urbanizing landscapes where rapid growth is leading to socioeconomic inequality, including a 30.8% increase in rent from May 2020 to May 2021 associated with rising evictions and homelessness (Schwedelson, 2021). Such rapid urban growth is associated with increased sprawl and disconnected road networks (Barrington-Leigh & Millard-Ball, 2020). Our results suggest that these dynamics will create habitat patches with conditions that favour puncturevine abundance. The municipal government, community organizations and stakeholders already recognize that puncturevine poses a serious problem for active transportation by disincentivizing bicycle travel. As urban growth pushes economically marginalized populations towards the city's periphery, puncturevine may have increasingly detrimental consequences for people that are reliant on bicycle transport for commuting yet lack access to recreational bicycling and its associated health benefits (Lee et al., 2017). Beyond our focal city, socio-ecological feedbacks between puncturevine population dynamics and urban systems are broadly representative of other pest and pathogen species that benefit from structural inequality (Des Roches et al., 2021; Halsey et al., 2023; Schell et al., 2020). Mapping and modelling efforts that identify where harmful organisms spread in urban ecosystems are an essential starting point for more equitable and effective control measures.

AUTHOR CONTRIBUTIONS

T. Trevor Caughlin conceived the study, analysed data and wrote the first draft of the paper. Martha M. Brabec helped create the study design and provided feedback to interpret the results. Matthew Clark, Louis W. Jochems, Nick Kolarik, Andrii Zaiats and Cody Hall collected field data and developed GIS data layers. Jason M. Winiarski, Breanna F. Powers and Kelly Hopping aided sampling efforts. All authors contributed to drafts of the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

No authors have any conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Novel data collected for this study are available at https://doi.org/10.7923/s3mm-v098 (Caughlin et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Workflows used to construct the puncturevine abundance, emergence and persistence datasets.

Figure S2. Posterior distributions for predictor variables from generalized linear mixed-effect model for puncturevine persistence. The location of each posterior distribution relative to zero (indicated by a vertical line) indicates whether the predictor had a positive or negative impact on abundance. The interaction term refers to an interaction between street betweenness and bare ground. Wider posterior distributions indicate higher uncertainty.

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