Research Article

Mapping Low-Elevation Species Richness and Biodiversity in the Eastern Mojave Desert

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ABSTRACT

Global loss of biodiversity is a well-known concern for conservationists and managers, but detailed spatial maps of local biodiversity for use by local managers are often lacking. We used a suite of existing species distribution models to calculate spatial variation in low-elevation species richness across Clark County, Nevada, USA, comprising much of the eastern Mojave Desert. We then used a macroecological model to estimate true latent low-elevation biodiversity across the county, correcting for potential taxonomic bias in the estimates of species richness. We found that species richness and biodiversity tended to be higher along the Muddy and Virgin Rivers and in the Las Vegas valley. Biodiversity was positively associated with flat, rocky landforms, low elevation, late seasonal greenup, and lower differences between winter and summer temperature. We present a brief example for local managers to apply the new publicly available low-elevation species richness and biodiversity spatial layers.

Index terms: biodiversity; Las Vegas; Mojave Desert; species distribution model; species richness

INTRODUCTION

Human population growth and land development continue to have expanding impacts on species persistence across the globe (Tilman et al. 2017). Efforts to offset these effects are also expanding, but information on where to apply these efforts is critical to ensure that the maximum positive benefit is achieved (Zellmer et al. 2019). Biodiversity is one metric commonly targeted for protection or conservation in order to maximize the benefit of conservation actions, including those conducted at small scales (Cardinale et al. 2012; Wintle et al. 2018). Monitoring biodiversity over time can be challenging, as monitoring species diversity can miss replacement of native species with invasive species if managers do not pay particular attention to the component species (Hillebrand et al. 2017). However what can still be beneficial is estimating biodiversity across space. Land managers and conservationists often need to know where to conduct conservation activities such as land protection and habitat restoration (e.g., Stoms et al. 2013). For single species of concern, these areas are often known based on local experience. But if the goal is general benefit to a wide variety of species, local knowledge of where the highest number of species will overlap in their distributions is often unknown.

Clark County, Nevada, USA, is a good example of a place needing information on spatial patterns in biodiversity. Clark County has experienced long, sustained growth in its human population, from \sim 270K residents in 1970 to \sim 2.27M in 2020, with the majority of people (>1.8M) living in the metropolitan area of Las Vegas (USCB 2012, 2022). The county population is forecast to grow to 2.7M by 2030 and over 3M by 2045 (UNLV 2020). Along with this growth has come degradation to plant and animal populations and their habitats. Degradation has occurred primarily at lower elevations within the county because

most private land, and thus development, population growth, and spillover degradation, occurs at these lower elevations. At lower elevations, much attention has been given to individual species, especially the federally listed threatened Mojave desert tortoise (Gopherus agassizii), listed in 1990 (USFWS 1990). At the time of listing, specified threats to desert tortoise persistence included habitat loss/conversion, grazing, and off-road-vehicle use and these threats are ongoing (USFWS 1990; Darst et al. 2013). There are also several other species of conservation concern, including the federally endangered southwestern willow flycatcher (Empidonax traillii extimus; USFWS 1995), the federally threatened vellow-billed cuckoo (Coccvzus americanus; USFWS 2014), and state-protected plants Las Vegas bearpoppy (Arctomecon californica), threecorner milkvetch (Astragalus geveri var. triquetrus), blue diamond cholla (Cylindropuntia multigeniculata), and sticky buckwheat (Eriogonum viscidulum). For the conservation of these and other species, Clark County, Nevada, implements a multiple species habitat conservation plan to mitigate private land development focused on mitigating habitat loss at low elevations (i.e., <1220 m), in compliance with the U.S. Endangered Species Act (Clark County 2000). This plan covers 78 species, whose common features are conservation concern and occurrence below 1220 m (\sim 4000 ft) in elevation. Much conservation modeling is now spatially explicit and particularly common is the use of species occurrences to develop such probabilistic models (species distribution models, SDM). Both external sources and Clark County have commissioned SDMs for the species covered under the multiple species habitat conservation plan, and there is a need for spatially explicit estimates of species richness to best implement this plan.

In addition to a targeted list of species of concern, there is also growing interest in supporting conservation actions that benefit biodiversity in general. In order to translate that interest into on-

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the-ground actions to benefit biodiversity, land managers need to know where to prioritize actions. Our goal in this project was to provide spatially explicit estimates of species richness and biodiversity across Clark County at elevations <1220 m. Our first objective was to create an index of species richness across the available species set, which focused on low-elevation species covered under the multiple species habitat conservation plan (a stacked SDM, i.e., SSDM; Calabrese et al. 2013). We used existing probabilistic models of mammal, avian, reptile, invertebrate, and plant occurrence across the county to generate two continuous predictive layers. In regard to general biodiversity, this method has been shown to be subject to some ecological and taxonomic bias resulting from the inclusion and choice set of individual species (Calabrese et al. 2013). Therefore, our second goal was to build a macroecological model explaining spatial variation in our species richness index to "correct" for accumulated bias deriving from species' inclusion in our input dataset, assuming some basic macroecological principles within the eastern Mojave Desert (Calabrese et al. 2013; Fithian et al. 2014). The assumption of basic macroecological principles is that there are emergent coarse-scale statistical relationships between species occurrence and diversity and myriad local abiotic and biotic factors that are themselves associated with regional patterns (Smith et al. 2008). We relied on previous research to select the five most important macroecological factors underlying the distribution of 15 species of amphibians, reptiles, mammals, and invertebrates in the Mojave Desert (Inman et al. 2014). We refer to this model as the lowelevation biodiversity index because it "corrected" our species richness index. Here, we describe and present both the listspecific species richness index and the macroecologically adjusted biodiversity index as publicly available layers in a Geographic Information System (GIS) for conservation and land manager use across Clark County to maximize the net benefit of future land use and habitat restoration actions. Finally, we provide an example using the biodiversity model in a GIS to demonstrate its use to maximize protection of biodiversity.

METHODS

Study Area

The Mojave Desert is a North American desert in the southwestern United States (Figure 1). Precipitation patterns exist along a gradient, with the western Mojave drier and experiencing winter rains and the eastern Mojave wetter with both winter rain and snow and summer monsoon rains (Germano et al. 1994; Keeler-Wolf 2003; Pietrasiak et al. 2014). At low elevations in the eastern Mojave Desert, precipitation can average 11 cm per year (Abella et al. 2009). Mojave Desert landforms are typically alluvial fans and basins, dominated by the creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) shrub alliance at lower elevations, blackbrush (*Coleogyne ramosissima*) shrub communities at middle elevations (>1100 m), and pinyon-juniper (*Pinus-Juniperus*) forests at higher elevations (>1800 m; Keeler-Wolf 2003; Abella et al. 2009; S. Cambrin, unpub. data).

Clark County is the southernmost county in the U.S. state of Nevada and encompasses \sim 20,800 km², covering much of the

eastern Mojave Desert (Figure 1). Approximately 88.9% is federally owned and managed with the remainder being state or private land. Elevation ranges from 137 m to 3634 m (Abella et al. 2009). Riparian shrub communities (e.g., Salix spp., invasive Tamarix ramosissima) occur along the Virgin and Muddy Rivers in the northeastern portion of the county. Approximately 12,800 km² are designated under some minimal type of conservation management, such as wilderness areas, federally protected lands, military lands, or state parks (Clark County Desert Conservation Program, unpub. data). Included within the conservation acreage is the Boulder City Conservation Easement (BCCE), a 353 km² area managed by Clark County to protect habitat for Mojave desert tortoises and other species and which we used as an example of applying the species richness and biodiversity layers derived here (Figure 1). Anthropogenic activities on public lands can be extensive, including off-road vehicles, shooting, and illegal dumping. As one example of quantifying anthropogenic activities, from 1995 to 2006 an average of nine million people annually visited the Lake Mead National Recreation Area along the eastern border of Clark County (Figure 1; Abella et al. 2009).

Conceptual Treatment of SDMs

SDMs represent a spatial product that can be derived using a variety of statistical methods and input data, ultimately resulting in spatially explicit predictions of the probability (usually relative probability) of species occurrence as a function of input spatial variables (Elith and Leathwick 2009). As of 2018, the Clark County Desert Conservation Program had either commissioned or had access to SDMs for 55 plant, reptile, mammal, avian, and invertebrate species. The list of species chosen for deriving SDMs was not comprehensive of all species present within Clark County, but was reflective of species occurring at low elevations that were most subject to degradation from private land development and were covered under the multiple species habitat conservation plan. Therefore, the resultant estimates of richness should be interpreted as richness of lowelevation species, hereinafter "species richness." Importantly, we then used the species richness layer and landscape data to generate a macroecological model generalized to all lowelevation species, and hereinafter refer to this predictive layer as "biodiversity" (Calabrese et al. 2013). All included SDMs were produced using Maxent (Phillips et al. 2006), logistic regression of presence-background points (Aarts et al. 2012), or an ensemble of random forest, generalized additive, and Maxent models (Appendix Table S1). All ensemble models (75% of the final SDMs) used k-fold cross-validation to evaluate SDM goodness-of-fit. The remaining models did not present validation methods or metrics in their associated reports, but did provide expert evaluation of SDM predictions by species experts.

Data Processing

Our first step in data processing was to classify all SDMs into one of three categories: suitable for use as provided (i.e., a continuous estimate of the relative probability of occurrence, scaled between zero and one), suitable for use after processing (e.g., species density estimates that can be scaled between zero and one), or unsuitable for this task (e.g., vector layers with



Figure 1.—Clark County, Nevada, USA, highlighting variation in lower elevation around the metropolitan area of Las Vegas. The Boulder City Conservation Easement was established in 1995 to protect habitat for Mojave desert tortoises (*Gopherus agassizii*) and other species. Elevations above 1220 m are masked out as white.

qualitative classification of species' occurrence or a probability raster that was only generated for a small portion of Clark County). All "suitable for use as provided" SDMs were developed using presence-background data (Aarts et al. 2012), with presence data representing a mix of reliable historic observations and observations from field work. For SDMs with density estimates that were all less than 1, the direct density estimate was retained as approximately equivalent to the probability of occurrence in that habitat cover type (i.e., low average observed densities = low probability of occurrence in a given plot). For density estimates that exceeded 1, densities were rescaled to a zero-to-one scale by dividing the observed value by the maximum value rounded up to the nearest tenth place to ensure all values were less than 1. In practice, this used scaled predicted density as a proxy for relative probability of occurrence for four species, an assumption that we were unable to test.

Simple spatial re-projection, raster snapping, or raster resampling were applied where necessary to standardize all of the SDMs to the same resolution (i.e., $250 \text{ m} \times 250 \text{ m}$), raster origin



Figure 2.—Example of the process for stacking species distribution models for individual species into a single quantitative predictive layer of species richness (i.e., biodiversity).

coordinates, and coordinate system (i.e., NAD83 UTM Z11N). All NoData cells were assigned a value of 0 prior to stacking. Some SDMs were resampled to a higher resolution (250 m) than that of the original SDM (1 km). In practice this meant that a grid cell that was previously 1 km \times 1 km with a single raster value now was composed of four grid cells, each 250 m \times 250 m, and each with the same original raster value. In terms of spatial accuracy this falsely implies a higher resolution at the level of the individual SDM, but we decided it was acceptable to do at the level of the SSDM because it allowed them to accommodate the resolution of the 250 m SDMs. This approach maximized inclusion of all information from the highest resolution SDMs. Some of the avian SDMs were generated at an even higher resolution than 250 m \times 250 m. These were resampled to a 250 $m \times 250$ m resolution taking the maximum value within the window to reflect the highest probability that a species was observed within the larger window. After processing, all SDMs were a continuous, probabilistic probability of species occurrence, or p-SDM (Calabrese et al. 2013).

Stacking p-SDMs and Macroecological Model

Next we "stacked" all of the p-SDMs together via summation over overlapping grid cells, yielding a continuous index of species richness (a p-SSDM; Figure 2), a method that has been found to be robust and accurate when compared with validation data (Calabrese et al. 2013; Zellmer et al. 2019; Zurrell et al. 2020). The stacked p-SSDM is useful in that it retains information on the input species, but there is a potential for bias in the p-SSDM with regards to true biodiversity depending on the level of latent bias in which species were chosen for creation of the individual SDMs (Distler et al. 2015). For example, if only reptile species were used for the species richness model, that model may not represent biodiversity of plants. To resolve this we conducted a second analysis, whereby we built a macroecological model that sought general rules in the eastern Mojave Desert driving species assemblages (Calabrese et al. 2013; Distler et al. 2015). We used linear regression to model the p-SSDM species index as a function of environmental predictors. The environmental predictor variables were chosen from the five most important variables identified by Inman et al. (2014) in a study on SDMs for 15 amphibian, reptile, mammal, and invertebrate species across the Mojave Ecoregion. The five predictor variables used in this macroecological model were elevation, seasonal thermal difference (i.e., the difference between winter and summer surface temperatures), surface texture (i.e., an index of sandy versus rocky surface), topographic position (i.e., high values equal valley bottom while low values equal mountain or ridge top), and seasonal greenness timing (i.e., the average date of maximum vegetation greenness) (Table 1). Winter precipitation was a sixth environmental predictor variable initially included. However, winter precipitation was highly correlated with elevation (r = 0.863) and was excluded from further analysis because previous work has shown elevation to be a primary driver of regional variation in biodiversity (Mateo et al. 2012). Inman et al. (2014) used generalized additive models and machine learning (i.e., Maxent) to develop their ensemble SDMs (not used in our analysis). Their models were validated using independent data and Akaike's Information Criteria, Bayes Information Criteria, the Boyce Index, the area under the receiver operating characteristic curve, and expert judgement on the plausibility of partial response curves for the environmental predictors. We considered the top variables across all 15 species to be sufficiently representative of macroecological patterns in the Mojave Desert for use in our macroecological model.

We then generated a systematic grid of sample points 2.25 km apart from each other to sample the p-SSDM species richness raster and the environmental predictor variable rasters while

Table 1.—Environmental predictor variables used in creation of the macroecological biodiversity model. Variables were the five most influential variables for species distributions in the Mojave Ecoregion (Inman et al. 2014).

Variable	Unit	Description	Source
Elevation	m	Elevation calculated using remote-sensed data	USGS National Elevation Dataset
Seasonal thermal change	Index	Higher values indicate higher disparity between summer and winter temperatures	Inman et al. 2014
Surface texture	$^{\circ}\mathrm{C} \times 100$	Difference between mean daytime and nighttime surface temperatures	Inman et al. 2014
Topographic position	Index	Steady state wetness index as a function of both slope and the upstream contributing area per unit width orthogonal to the flow direction	USGS National Elevation Dataset
Seasonal greenness timing	Time	Date of the maximum value of the Normalized Difference Vegetation Index	Inman et al. 2014

ensuring even coverage across the county and minimizing spatial autocorrelation. After removing points from the sample grid that fell within "disturbed" areas (i.e., graded or paved construction as determined from aerial imagery analysis; L. Bice, unpub. data) there were 3827 sample points. We then used linear regression in Program R 3.5 (R Core Team 2018) to derive the macroecological statistical model (*speciesrichness* ~ $\sum_{j}^{I} \beta_{j} x_{ji} + \varepsilon_{i}$, where β are coefficient estimates relating species richness to each of the five *j* covariates in grid cell *i* with residual error ε). Finally, we used the coefficients from the statistical model in Raster Calculator in ArcGIS 10.4 (ESRI, Redlands, California, USA) to create the continuous biodiversity predictive surface. All environmental raster layers were available at a resolution of 1 km, so the output macroecological layer is at this resolution as well.

Example - Reserve System Design

We present an example to show how the p-SSDM species richness and macroecological biodiversity models can be used in designing a new reserve system or in assessing the effects of land management. We created two hypothetical identically sized units where the question is placement within a portion of northeast Clark County or evaluating the effects of a management action within either unit. Finally, we calculated zonal statistics for the BCCE to show how the current BCCE is related to both the species richness and biodiversity models.

RESULTS

Initial processing for quality control resulted in 29 SDMs being classified as suitable, 11 SDMs classified as suitable after processing, and 15 SDMs classified as unsuitable (Appendix Table S1). SDMs from 9 mammal, 11 bird, 6 reptile, 1 invertebrate, and 13 plant species were eventually suitable for inclusion. Most SDMs classified as unsuitable were plant SDMs that only contained qualitative estimates of survey results (e.g., "found," "surveyed but not found," and "not surveyed"). These SDMs provided qualitative information to which probabilities could not be assigned (e.g., "not surveyed" does not equal "not present"). A couple of unsuitable SDMs were originally generated only for a small subset of Clark County (e.g., portions of the Virgin River), and because they did not include occurrence probability estimates elsewhere, were unsuitable due to their minimal spatial extent.

The output p-SSDM shows spatial variation in species richness, with any given portion of the county predicted to have between 2 and 19 of the 40 modeled species, on average (Figure 3). General patterns in biodiversity of the 40 species showed higher richness at lower elevations in Clark County, particularly along the Virgin and Muddy Rivers and surrounding the Las Vegas valley.

The macroecological regression model found that biodiversity decreased as seasonal thermal difference increased (β –0.003, SE 0.0005, P < 0.001), biodiversity increased as surface texture increased (i.e., became rougher; β 0.002, SE 0.0003, P < 0.001), biodiversity increased as topographic position increased (i.e., became flatter; β 0.065, SE 0.019, P < 0.001), biodiversity

decreased as elevation increased (β –0.002, SE 0.00009, P < 0.001), and biodiversity increased as the date of maximum vegetation greenness increased (β 0.328, SE 0.032, P < 0.001). Altogether, the five variables explained 27.7% of the variation in species biodiversity (Adjusted R^2 = 0.2768).

General spatial patterns of biodiversity were similar to the species richness model in that biodiversity was predicted to be higher in low-elevation portions of the county (Figure 4). The Muddy and Virgin River corridors, while still predicted to have high general biodiversity, did not stand out as much as strong centers of biodiversity as they did in the species richness model.

The hypothetical reserve units provide an example of how the species richness and biodiversity layers can be used for on-theground conservation. Unit A had a 15.7% higher average score for the species richness model (9.6 vs. 8.3) and a 12.0% higher average score for the biodiversity model than unit B (10.3 vs. 9.2). The summed index values for biodiversity were 455.3 and 404.3 index units in units A and B, respectively. Aside from hypothetical applications, the established BCCE conservation area had an average species diversity value 6.4% higher than the county-wide average (10.0 vs. 9.4) and a biodiversity score 10.6% higher than the county-wide average (10.4 vs. 9.4).

DISCUSSION

Managing for species richness and biodiversity can be challenging due to a lack of data on where the highest number of species may co-occur. For Clark County, Nevada, in the eastern Mojave Desert, we leveraged multiple species distribution models for bird, reptile, mammal, plant, and invertebrate species to calculate a continuous surface of species richness, with a focus on species occurring at lower elevations within the eastern Mojave Desert. We then used macroecological patterns underlying low-elevation species richness to predict low-elevation biodiversity across Clark County. We found that in the 140-1220 m elevation zone considered here that biodiversity was higher at the lowest elevations, flat locations with rockier surfaces, areas with later vegetation greenup, and areas with lower temperature differentiation between winter and summer. We focused on lowelevation species to make the tool most applicable for lowelevation land development and to be used to offset lowelevation anthropogenic stressors that spill over from cities, including habitat degradation and loss and subsidized synanthropic predators (Kristan and Boarman 2007; Darst et al. 2013; Zylstra et al. 2013).

Different types of biodiversity in the Mojave Desert have been addressed in various ways previously, finding patterns that agree with those we found here. For example, plant and biological soil crust community diversity is higher on geomorphic landforms with rocky surfaces or shrubs (Pietrasiak et al. 2014). As a function of elevation, bryophyte and lichen species diversity is highest at lowest elevations, and perennial shrub density is lowest at high elevations (Thompson et al. 2005). Similar to our findings for both species richness and biodiversity, riparian areas in Clark County support higher butterfly diversity (Fleishman et al. 2005). Within the Muddy River (northeast Clark County), bird species richness is positively associated with total vegetation volume (Fleishman et al. 2003). And while our models were



Figure 3.—Species richness for the 40 low-elevation species used to build the stacked species distribution model (p-SSDM). Index represents the expected number of the 40 species to occur at a location as a function of the probability of each individual species occurring at that location. Areas masked in white are over 1220 m in elevation.

temporally static, previous work in the Mojave Desert has found that temporal changes in plant species diversity are driven by drought and precipitation (Lei 1999).

For land managers, our species richness and biodiversity predictive surfaces can be used in a variety of ways. For example, the Mojave Desert is subject to rapid development of renewable energy at its lower elevations, particularly solar farms, and knowledge of where developments would cause the lowest loss of biodiversity would be highly beneficial (Cameron et al. 2012; Stoms et al. 2013). When development does happen, spatially explicit low-elevation species richness or general low-elevation biodiversity that is lost in order to guide offsetting actions (i.e., mitigation; Kreitler et al. 2015). And when planning for future climate change, identifying areas of high biodiversity that are also expected to be somewhat robust to changing temperatures and precipitation regimes (e.g., woodlands and areas near water) can be crucial to protecting future biodiversity (Rich et al. 2019). The hypothetical reserve units demonstrate these applications. For example, if setting up a new conservation area, unit A would be expected to benefit a higher diversity of species than unit B. Alternatively, if unit B was set for energy development and a 1:1 biodiversity mitigation ratio were desired, 404.3 biodiversity index units could be protected elsewhere.

Our species richness model here is naturally limited by the low-elevation species and taxonomic groups for which high resolution, spatially explicit, and probabilistic species distribution models were available, potentially biasing our finding of



Figure 4.—Map of predicted low-elevation biodiversity in Clark County, Nevada, including an existing conservation easement and two hypothetical conservation areas (A and B). Biodiversity estimates were derived using the 40-species species richness model to derive general low-elevation macroecological patterns in underlying biodiversity. Masked white areas are above 1220 m in elevation.

higher species richness at lower elevations. However, there may be some instances where the limited scope of species richness is actually preferred to general biodiversity. For example, land management often focuses on maximizing conservation value to a subset of all species (e.g., local species of conservation concern, management indicator species). Thus it may be more advantageous to design a reserve system or quantify lost species richness by focusing on as many of the desired subsets of species as possible, as opposed to a reserve system that has the highest total biodiversity but neglects many of the species of specific interest. Such is the case in Clark County, where the county implements a multiple species habitat conservation plan in compliance with the U.S. Endangered Species Act. This plan covers conservation of 78 species, many of which were included in our analysis of species' richness. Other taxonomic scales of richness may also be of interest, such as soil microorganism diversity (Parker 2010) or bryophyte and lichen soil crusts (Thompson et al. 2005). We expect that as spatially explicit modeling of species distributions advances, and the diversity of species for which probabilistic models of occurrence increases, future estimates of biodiversity will improve the options for taxonomic species richness, inclusiveness, and specificity.

The availability of SDMs may seem like a panacea for spatially explicit biodiversity conservation, but we caution that users need be circumspect in their use of existing SDMs. Poor statistical practice can produce inaccurate or biased SDMs, which cannot be remedied during the "stacking" phase. SDMs should also be continuous predictions of the relative probability of a species' occurrence, not an arbitrary binning such as "likely present" versus "likely absent" (e.g., above or below 0.5; Calabrese et al. 2013). For our purposes, the majority (75%) of our input SDMs were high quality, composed of well-validated SDMs built under a robust and open analytical framework (Southwest Ecology 2018), enabling us to use them to generate spatially explicit estimates of species richness and ultimately biodiversity. With care, other practitioners may obtain similar high-quality SDMs for uses similar to those presented here. We also note that our "borrowed" macroecological predictor variables were developed for a species set that excluded avian species (Inman et al. 2014). Nonetheless, we considered them sufficient given their good validation for amphibian, reptile, mammal, and invertebrate species and that other studies have found similar predictors to be important drivers of macroecological patterns in avian species (Mateo et al. 2012).

It is also worth noting that biodiversity is but one of many challenges facing conservationists. Individual species' persistence also matters, both for those species' persistence and for a meaningful treatment of biodiversity as a conservation goal. For example, trends in the number of species observed can be constant, yet mask complete species turnover (Hillebrand et al. 2017). Several of the species in our dataset are legally protected for their own preservation, and focusing solely on species richness or biodiversity would miss how individual species' populations are faring. Thus we suggest that the species richness and biodiversity layers presented here be used as a tool in addition to individual species management for the management and conservation of lower elevation landscape in the eastern Mojave Desert ecosystem.

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Open Research Statement

The species richness and biodiversity layers are available on Data Dryad at https://datadryad.org/stash/share/oiGtwGiz_nDBSOG_PUoUkKLAhayDJh-9iPFAh6TID5g.

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