

Community Ecology

Variation in the community composition of blow flies (Diptera: Calliphoridae) in neighboring deserts within Joshua Tree National Park

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Joshua Tree National Park (JOTR) in southern California offers a unique opportunity to explore insect biodiversity across 2 distinct desert ecosystems: the lower-elevation Sonoran Desert and the higher-elevation Mojave Desert. In these harsh environments, many blow flies (Diptera: Calliphoridae) serve as important decomposers, feeding on animal waste and decomposing tissue. Some blow fly species, notably non-native species, are associated with human activity, which underscores the need to study their communities in JOTR, where annual visitation has reached 3 million. This study investigated the community composition of blow flies across the park and assessed the impact of visitor activity on blow fly communities in JOTR. Sampling from 2021 to 2023 using traps baited with squid carcasses revealed higher blow fly diversity in the Mojave Desert relative to the Sonoran Desert, in contrast to previous insect and vegetation surveys within the park. Across the park, blow fly community composition (i.e., β -diversity) differed by season. Blow fly abundance, richness, and diversity were similar between low- and high-visitor activity sites. However, more non-native species were collected in areas of low visitor activity, suggesting regular waste removal practices in high-visitation sites might limit their ability to complete development as secondary colonizers. This study is the first to characterize blow fly communities in Joshua Tree National Park. These findings demonstrate that blow fly communities reflect previously established park boundaries and underscore the importance of waste management practices in reducing the spread of non-native species throughout the park.

Key words: decomposition ecology, forensic entomology, ephemeral resource patch, human disturbance, southern California, non-native

Graphical Abstract

(1) Do blow fly communities differ between neighboring deserts?

Yes, **temporally** and **spatially**...

Mojave Desert differed from the transition zone and Sonoran Desert.

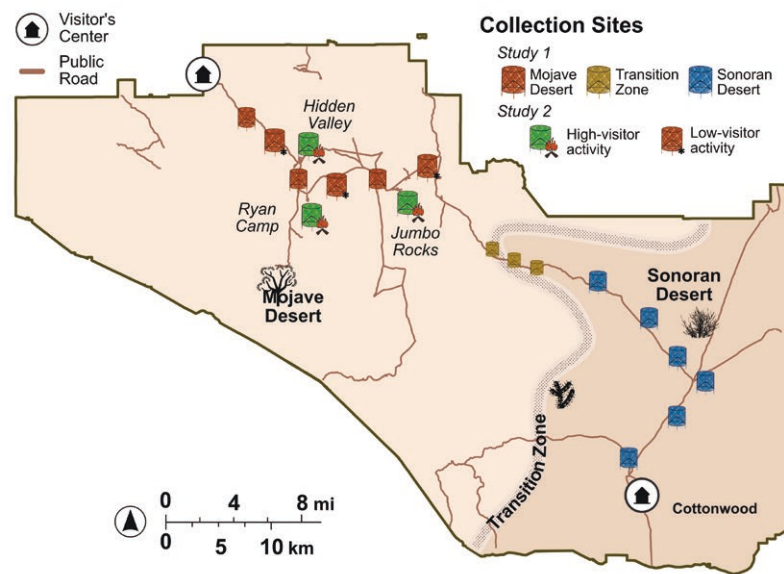
(2) What is the impact of human activity on blow fly communities within protected areas?

Community composition did not differ



Species richness significantly differed between **seasons** but did not differ between visitor activity level sites.

Joshua Tree National Park Map



County of Riverside, California State Parks, Esri, HERE, Garmin, SafeGraph, FAO, METI/NASA, USGS, Bureau of Land Management, EPA, NPS

Introduction

Blow flies (Diptera: Calliphoridae) rely on ephemeral resource patches, such as carrion, live animal tissue, and fecal matter, to reproduce and complete development (Byrd and Tomberlin 2020). To effectively detect and colonize these unpredictable and variable resources, blow flies have evolved sensitive olfactory and visual resource detection capabilities, along with strong dispersal ability (Wall and Fisher 2001, Oliveira and Vasconcelos 2020). Plasticity in their development and behavior enables blow flies to adapt to challenging environmental conditions, including stressful temperatures, which contributes to their widespread success (Tarone and Foran 2006, Owings 2012, Rusch et al. 2020, Carmo et al. 2022).

These life-history traits have associated many blow fly species with death investigations, as they are often the first arthropods to arrive in carrion (Byrd and Tomberlin 2020). Their larval development is highly influenced by environmental conditions, namely temperature, which can be used to estimate a minimum post-mortem interval (mPMI); this is commonly referred to as time since death (Tomberlin et al. 2011). Additionally, the blow fly species present on carrion may reveal where the death occurred and whether a body has been relocated based on regional species records (Byrd and Tomberlin 2020). Thus, a shared goal between forensic entomologists and ecologists is to understand how the environment influences blow fly community assembly. To address these knowledge gaps, especially in understudied regions like deserts, we can apply ecological frameworks to improve our understanding of blow fly communities in the context of forensic entomology (Tomberlin et al. 2011).

Joshua Tree National Park (JOTR) spans the lower elevation Sonoran Desert and higher elevation Mojave Desert in southern California, offering a unique location to study blow fly community assembly along an arid environmental gradient. The National Park Service (NPS) and United States Geological Survey (U.S. Geological Survey (USGS) 2024) established these 2 deserts as distinct ecoregions within the park, connected by a transition zone (Sadler et al. 2018, NPS 2023). Ecoregions, defined as “areas of

general similarity in ecosystems and in the type, quality, and quantity of environmental resources,” provide a spatial framework for research and ecosystem management (Omerik and Griffith 2014). The 2 deserts within JOTR recognized by the NPS are not delineated based on the USGS ecoregion boundaries; however, they are still recognized by both the NPS and USGS as distinct deserts. The Sonoran Desert is characterized by low elevations (<2,000 feet), low precipitation, and high temperatures (U.S. Geological Survey (USGS) 2024). Notably, vegetation in this region consists of ocotillo (*Fouquieria spp.*), smoketree (*Psoralea spp.*), and cholla cactus varieties (*Cylindropuntia spp.*). The Mojave Desert is characterized by a milder climate compared to the Sonoran Desert and contains thousands of Joshua Trees (*Yucca brevifolia*) that are native to this region (U.S. Geological Survey (USGS) 2024).

To reinforce ecoregion delineations, researchers have suggested including insect assemblages in defining ecoregions (Munguía-Ortega et al. 2021). Only 2 studies to date have examined insect assemblages within JOTR, providing limited information about differences in insect communities between the 2 deserts (Buffington and Gates 2013, Sadler et al. 2018). The most recent insect study completed in JOTR sampled aculeate wasps (Hymenoptera: Chyphotidae, Brachycistidinae [Tiphidae], and Mutillidae) along the park’s environmental gradient. This study reported spatial and temporal partitioning of several species and higher diversity in the Sonoran Desert compared to the Mojave Desert, supporting the current desert boundaries (Sadler et al. 2018).

Blow flies are widespread and play ecologically important roles as decomposers and pollinators, even in deserts, suggesting that they can be included in delimiting biogeographical areas (Munguía-Ortega et al. 2021). Exploring patterns in community composition in JOTR marks the initial steps toward disentangling the mechanisms contributing to community assembly in harsh environments. The absence of published records for blow fly species in JOTR presents a significant data gap necessary to study community assembly patterns of carrion insects in desert ecosystems and may hinder death

investigations that involve insect evidence in and around the park. The need for species-specific records becomes even more crucial considering incidents of visitors who go missing or die every year in the park (Urrea 2004, Nelson 2016, City News Service 2018, NPS 2019, Makinen et al. 2022, Williams 2024).

Though blow flies rely on naturally fragmented habitats, like carrion, it is unknown how increased anthropogenic disturbance affects the ability of blow flies to find or use suitable resources. Anthropogenic disturbance has been associated with biodiversity loss across many taxa (Cheptou et al. 2017) while natural fragmentation has been shown to promote resource competition and coexistence (Ives 1991, Rohlf and Hoffmeister 2004, Germain et al. 2018) and increase biodiversity (Butterworth et al. 2023). Within JOTR's natural desert ecosystem, there are 9 campgrounds that contain 500 campsites. These disturbed sites can provide a source of human waste that can act as reliable resources for blow fly development. The increasing and reliable resource availability in environments with high human activity (i.e., human food waste) may draw blow fly populations away from naturally occurring food resources, altering nutrient processing in the wild.

This study examines patterns of blow fly community composition across the desert gradient and of visitor activity (activity of humans and their companion animals) levels within JOTR. We measured blow fly species diversity, abundance, and composition and the abiotic factors that may influence their assembly in 2 neighboring deserts and their transition zone within the park with sampling conducted in both low- and high-visitor activity areas. We leverage the desert ecosystems within JOTR to address 2 questions: (i) Do blow fly communities differ between neighboring deserts? And (ii) What is the impact of human activity on blow fly communities within protected areas, like national parks? We expect that season and human activity will primarily influence the assembly of flies in desert environments, similar to previous studies in non-desert environments (Kirkpatrick 2007, Weidner et al. 2015, Babcock et al. 2020). Additionally, we expect community composition to significantly differ between each

desert and between sites with low- and high-human activity based on prior research that has demonstrated differences in arthropod community composition driven by land use, vegetation, climate, and anthropogenic disturbance (Crist et al. 2006, Kavazos and Wallman 2012, Zhu et al. 2014, Langer et al. 2019, Alvarenga et al. 2020, Babcock et al. 2020).

Methods

Preliminary Trap and Bait Testing

Following preliminary trap testing, a standing inverted cone trap (reusable Rid-Max Fly Trap; Big H Products, Inc., Idaho Falls, USA) was found to be the most appropriate trap based on collected species abundance, affordability, size, and preservation of flies for identification (Fig. 1a). The color and size of this trap also “did not attract attention or cause unauthorized impact to the environment,” as outlined in the NPS permit conditions. Though limited data are available for appropriate baits in arid environments within the United States, previous work has suggested whole squid carcasses as the most effective bait in arid environments due to its ability to maintain moisture (Baz et al. 2013, Brett et al. 2021). We compared fly capture in the park using traps baited with 200 g of pork liver, beef liver, or squid, all aged 3–4 d at -27°C before use in traps. In addition, horse manure was tested as bait due to observation of blow fly activity at horse manure within the park. The pork liver, beef liver, and horse manure baits did not capture more than 4 blow flies each. The aged squid attracted the greatest abundance and diversity of flies relative to the other baits tested and was used for subsequent trapping.

Sites

Joshua Tree National Park (JOTR) consists of 2 desert regions, the Mojave Desert (MD), the Sonoran Desert (SD), and a buffering Transition Zone (TZ) that connects the 2 deserts (Fig. 1b). To investigate the community composition of blow flies in Joshua Tree

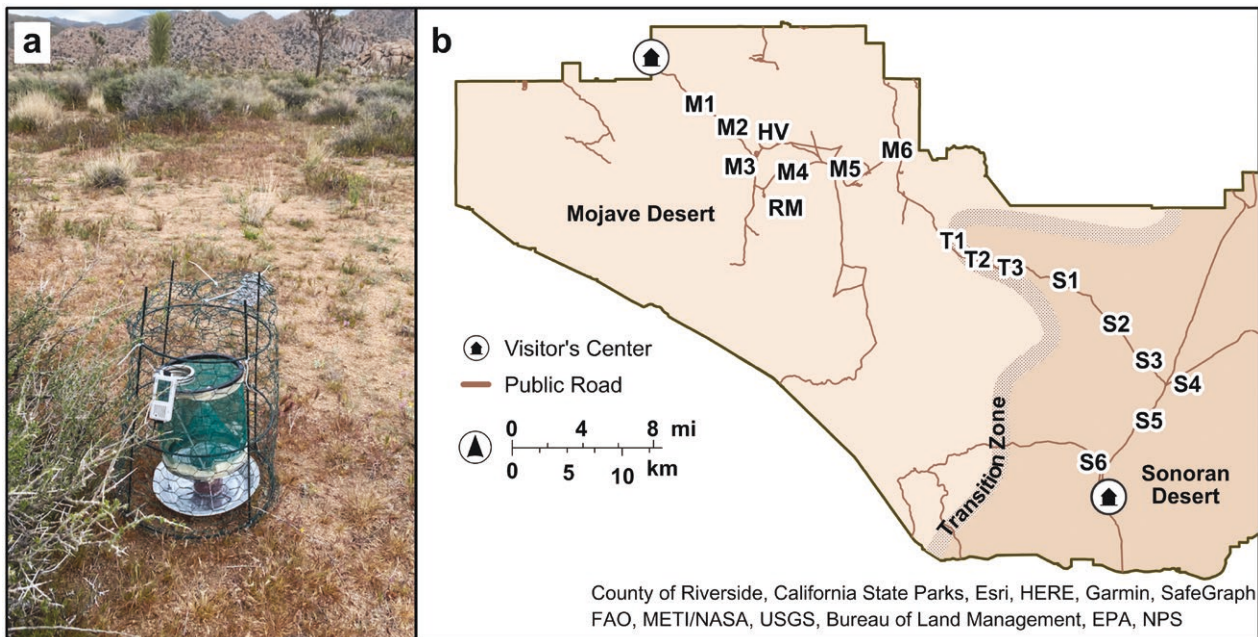


Fig. 1. (a) Trap set-up in park comprised of a pie pan with soapy water, squid bait in a mason jar, an inverted cone trap, a modified tomato cage cover, and a HOBOT data logger. (b) Map of JOTR with sites across the park. M = Mojave Desert; T = Transition Zone; S = Sonoran Desert. Numbers alongside letters are site identifiers. HV = Hidden Valley campground; RM = Ryan Mountain campground; JR = Jumbo Rocks campground.

Table 1. List of trap site locations and elevation. All high-visitor activity sites were in the Mojave Desert ecoregion. Note the decreasing elevation from the Mojave desert to the Sonoran Desert.

Site ID	Desert	Latitude	Longitude	Elevation (m)
M1	MD	34.05664786	-116.2223487	1,180
M2		34.05177419	-116.1876023	1,235
M3		34.01706372	-116.1628831	1,289
M4		34.01307964	-116.1258042	1,428
M5		34.01023375	-116.0791123	1,395
M6		34.02161672	-116.0317338	1,143
T1	TZ	33.94894771	-115.9734932	976
T2		33.93880726	-115.9511329	770
T3		33.93273352	-115.9308601	676
S1	SD	33.92105203	-115.8683524	531
S2		33.89254248	115.8204861	570
S3		33.85607376	-115.7805037	699
S4		33.83409149	-115.7596678	775
S5		33.80836038	-115.7793775	860
S6		33.76015222	-115.8204861	948
Ryan Mountain Campground (RM)	High-visitor activity sites	33.983585	-116.154896	1,317
Jumbo Rocks Campground (JR)		33.99167	-116.064966	1,340
Hidden Valley Campground (HV)		34.016191	-116.161663	1,283

MD = Mojave Desert; TZ = Transition Zone; SD = Sonoran Desert.

National Park, we selected a total of 18 field sites spanning the park (Table 1). Six collection sites were in the MD, 6 collection sites were in the SD, and 3 collection sites were in the TZ region because of limited road access across the TZ. Three additional campground sites that experience high-visitor activity (HV, RM, and JR) were also sampled in the MD region of the park to address the second research question. Low-visitor activity sites were the same as 3 of the MD sites used for the first objective. The high-visitor activity sites (campgrounds) were characterized by marked campground use that requires visitors to register for overnight stays. The campgrounds also contain large areas available for vehicle parking, pet activity, and at least 2 large dumpsters, and at least 2 vault toilets each. Sampling was completed at different times per each question. All collection sites were at least 4 km apart to reduce the likelihood of population overlap (Schoenly et al. 1991, de Souza et al. 2015) and at least 150 m from a major road.

Fly collections and identification

All flies were collected under permits #JOTR-2022-SCI-0015 and #JOTR-2023-SCI-0005 and were handled as required by the NPS Research Permit and Reporting System. Approximately 200 g of aged squid bait was placed into a 237-ml glass mason jar and the entire trap was placed into a 30 cm pie pan containing soapy water to prevent ant predation of captured flies. A tomato cage (84 cm tall) wrapped in chicken wire was placed over the trap to reduce vertebrate disturbance. A HOBO temperature/relative humidity data logger (ONSET UX100-003, Bourne, USA) was placed on each trap during collection times to record local temperatures and relative humidity. Shaded sites were selected at the time of trap placement, but the amount of sunlight experienced at each trap position/day was not recorded. Traps were placed out for 4–5 h between the hours 0800 and 1600. The cone was blocked with a paper towel and the traps were placed in large plastic bags to ensure no flies escaped during transport back to the laboratory. Once in the laboratory, the flies were knocked down in a freezer and immediately placed into 90% ethanol. The samples were later morphologically identified to species using published keys (Whitworth 2006, Jones et al. 2019).

To evaluate fly communities in the 2 deserts and TZ (whole park survey), flies were trapped from the whole park approximately monthly from June to October 2022, March to May 2023, and September to November 2023 (total of 10 trapping days). We were unable to sample from November 2022 to March 2023 due to heavy precipitation and flooding during this period which limited access to our sites. During 2022, no blow flies were captured during the hot summer months (June–August), so we did not sample in those months in 2023. We also did not capture any blow flies in March and October 2023.

To examine fly communities by level of visitor activity, flies were collected from high-visitor activity sites (campgrounds) as well as low-visitor activity sites (non-campgrounds) on 3 days during fall 2022 (October to early November), 4 days during spring 2023 (February to early May), and 3 days during summer 2023 (late May to July). Each sampling date was ~2 wk apart and did not overlap with sampling dates for the whole park survey. Low-visitor activity sites were away from roads and trails and did not show signs of visitor disturbance.

Data Analyses

All analyses were conducted in R (R Core Team 2023). Environmental differences were quantified using 6 locally measured environmental variables from the HOBO readers placed with each trap (minimum, maximum, and mean temperature and relative humidity) and 19 downloaded variables matching site coordinates from BioClim (Fick and Hijmans 2017; Supplementary Table S1). These 25 environmental variables were then normalized to the same scale using the scale function in R, which scales the columns of a numeric matrix to 0. A principal components analysis (PCA) of the 25 scaled environmental variables was conducted in the *STATS* package (version 4.3.2) to examine the contribution of each variable to the overall environmental variation across sites.

Differences in community composition (β -diversity) were analyzed with permutational multivariate analyses of variance (PERMANOVA) on dissimilarity matrices using “*adonis2*” in the *vegan* package. Sampling events that resulted in no collections were

excluded to calculate distance matrices for further analyses. Initial models including trapping year, season, and desert showed no significant differences in community composition between years and no interaction between year and desert (Supplementary Table S2), so fly collections were pooled for each site and season for all future analyses.

For each desert and season, we calculated overall relative abundance and species richness, and measured α -diversity using the Shannon-Wiener index (Shannon 1948). Species richness and α -diversity were analyzed by desert (MD, TZ, and SD) and by season (fall and spring) to address whether blow fly communities differed between deserts and seasons. Species richness and α -diversity were also analyzed by activity level (low-visitor and high-visitor activity) and season (fall, spring, and summer) to examine whether visitor activity influences blow fly communities. Species diversity was confirmed for normality ($P = 0.08$) using the Shapiro-Wilk normality test in the stats package (R version 4.3.2). To examine the effects of season and desert type or site type on α -diversity, a 2-way analysis of variance (ANOVA) was performed. Post-hoc pairwise comparisons were performed with estimated marginal means of α -diversity using the *emmeans* package. A Kruskal-Wallis rank sum test was used to examine the effects of season and desert type or site type on species richness. Significant results were then analyzed using a Dunn test (Dunn 1964). The effect of elevation on species richness was tested using a negative binomial generalized linear model in the *lme4* and MASS package (R version 4.3.2). The effect of elevation on species diversity was tested using a linear model.

Dispersion effects were evaluated using the “betadisper” function which calculates the sample distance to the group centroid of the Bray-Curtis dissimilarity matrix to test for differences in multivariate dispersion of community composition between desert and season (Oksanen et al. 2022, R version 2.6-4). Following dispersion effect analysis, a PERMANOVA (Anderson 2017) was conducted using “adonis2” in the *vegan* package (Oksanen et al. 2022, R version 2.6-4) to determine whether there was significant clustering based on desert and season and if there was an interaction between desert and season. If significance was detected, post-hoc analyses for pairwise comparisons were conducted using “pairwise.adonis” in the *vegan* package (Oksanen et al. 2022, R version 2.6-4). Composition was visualized using a non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity among deserts and seasons. The fit of the NMDS analysis was confirmed with the stress measure, in which a value of < 0.2 generally indicates a good fit (Clarke 1993).

To determine whether high-visitor areas were associated with a higher abundance of flies, a generalized linear mixed model was used. To compare the ratios of non-native to native species at the 2 site types, the raw counts of non-native species (*Chrysomya* spp.; Baumgartner 1993, Wells and Kurahashi 1997, Rosati and VanLaerhoven 2007) were divided by the remaining native species. To analyze the ratios across site type, a binary generalized linear model was used with site as a random effect.

To determine whether one or more species may be an indicator of each desert, an indicator species analysis (ISA) was conducted in the *indicspecies* package (De Cáceres and Legendre 2009, Seaverns and Sykes 2020). This analysis calculates a significance value through permutation and produces an ISA value between zero and one. A low value indicates that a species is either rare or similar in abundance across groups, whereas a value closer to one means that a species is either unique to one group or has a high relative abundance within a group (Seaverns and Sykes 2020).

Results

Over the 2 studies, a total of 2,699 calliphorid flies were collected, representing 6 genera and 12 species. Of the total, 909 individuals were collected for the whole park survey (Supplementary Table S3) and 1,790 individuals were collected for the comparison between low- and high-visitor activity areas. The 12 species collected throughout the studies include *Calliphora coloradensis* Hough, *Ca. latifrons* Hough, *Ca. livida* Hall, *Ca. terraenovae*, *Chrysomya megacephala* (Fabricius), *Ch. rufifacies* (Macquart), *Cochliomyia macellaria* (Fabricius), *Lucilia cuprina* (Wiedemann), *L. mexicana* (Macquart), *L. sericata*, *Phormia regina* (Meigen), and *Protophormia terraenovae* (Robineau-Desvoidy).

Species Composition and α -diversity

The most abundant species in the MD was *Ph. regina* and the most abundant species in the TZ and SD was *Co. macellaria* (Fig. 2). Eight species were present in both deserts and the transition zone: *Ca. coloradensis*, *Ca. latifrons*, *Ca. livida*, *Ch. megacephala*, *Ch. rufifacies*, *Co. macellaria*, *Lucilia sericata*, and *Ph. regina* (Supplementary Table S3).

Across the 3 desert regions, species richness was highest in MD in the fall (11 species) and lowest in MD and SD in the spring (7 species); however, these differences were not significant (Fig. 3a, Table 2, desert: $\chi^2 = 3.457$, $df = 2$, $P = 0.178$; season: $\chi^2 = 2.505$, $df = 1$, $P = 0.113$). In SD, species diversity was significantly lower in the spring compared to the fall ($P = 0.009$). There were no significant differences between season in MD ($P = 0.458$) and TZ ($P = 0.691$), but there is a pattern of decreasing species diversity along the north-south park gradient (Fig. 3b, Table 2). Elevation did not have a significant effect on species richness across seasons ($R^2 = 0.345$; $z = 1.832$; $P = 0.067$), nor on α -diversity (adj $R^2 = 0.292$; $F_{3,26} = 3.91$; $P = 0.7$) across JOTR.

High-visitor activity sites had an overall higher abundance of flies ($n = 1,105$) compared to low-visitor activity sites ($n = 685$), but this was not significantly different ($R^2 = 0.625$; $P = 0.23$). For both site types, the most relatively abundant species were *Ph. regina* and *L. sericata* (Fig. 4a). Species richness significantly differed between spring and summer but did not differ between visitor activity levels (Table 3, Fig. 4b). A similar pattern is seen in species diversity across both site types, but no significant differences were detected (Fig. 4c, Table 4, Supplementary Table S4).

Throughout the park, the non-native species *Ch. rufifacies* was most abundant in the fall and very rare in the spring (Table 2). This temporal variation is also reflected when comparing high- to low-visitor activity sites, where non-native species were most abundant in the fall (Table 5). Interestingly, there were negligible differences in the percentage of non-native species between low- and high-visitor activity sites, regardless of season (Table 5), and the low-visitor activity sites had higher counts of non-native species. However, there was also no significance in the ratios between low- and high-visitor activity level sites ($z = -1.528$; $P = 0.126$).

Environmental Variation Among Desert Regions

The deserts significantly differed based on the 25 environmental variables ($F_{2,26} = 21.18$; $P = 0.001$), with a significant difference between MD and SD ($R^2 = 0.64$; $P_{adj} = 0.003$), MD and TZ ($R^2 = 0.57$; $P_{adj} = 0.006$), and SD and TZ ($R^2 = 0.21$; $P_{adj} = 0.036$). The environmental PCA (Fig. 5a, Supplementary Table S5) revealed that PC1 accounted for 60.60% of the variation and was influenced most by the BioClim variables and elevation. Many of

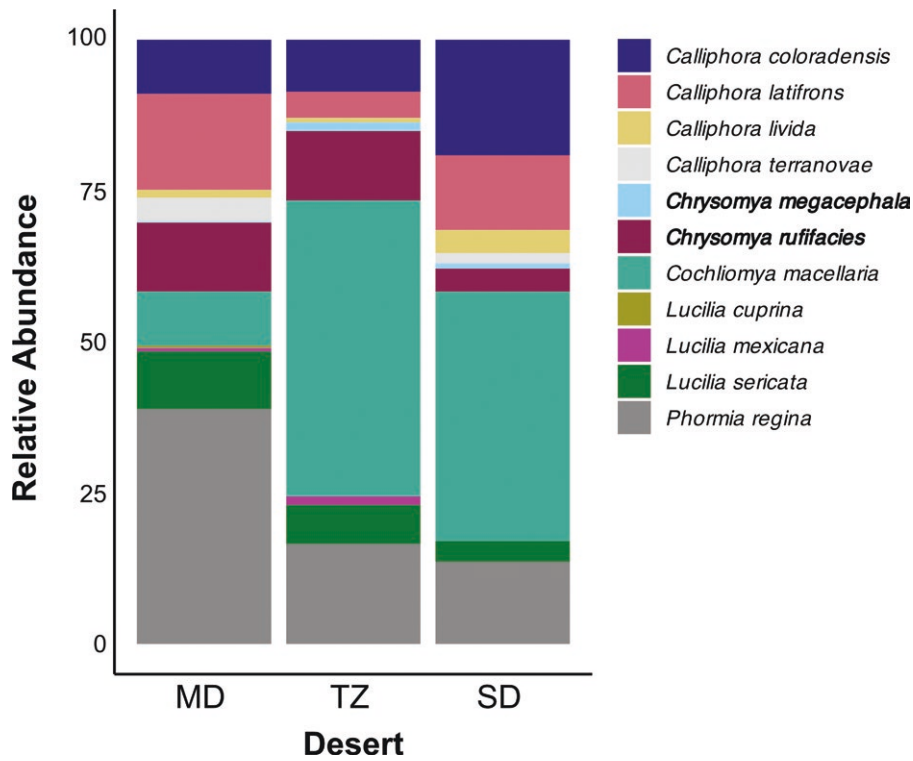


Fig. 2. The relative abundance of species found within deserts. Non-native species are bolded. TZ and SD are more similar in relative abundance compared to MD. MD = Mojave Desert, TZ = Transition Zone; SD = Sonoran Desert

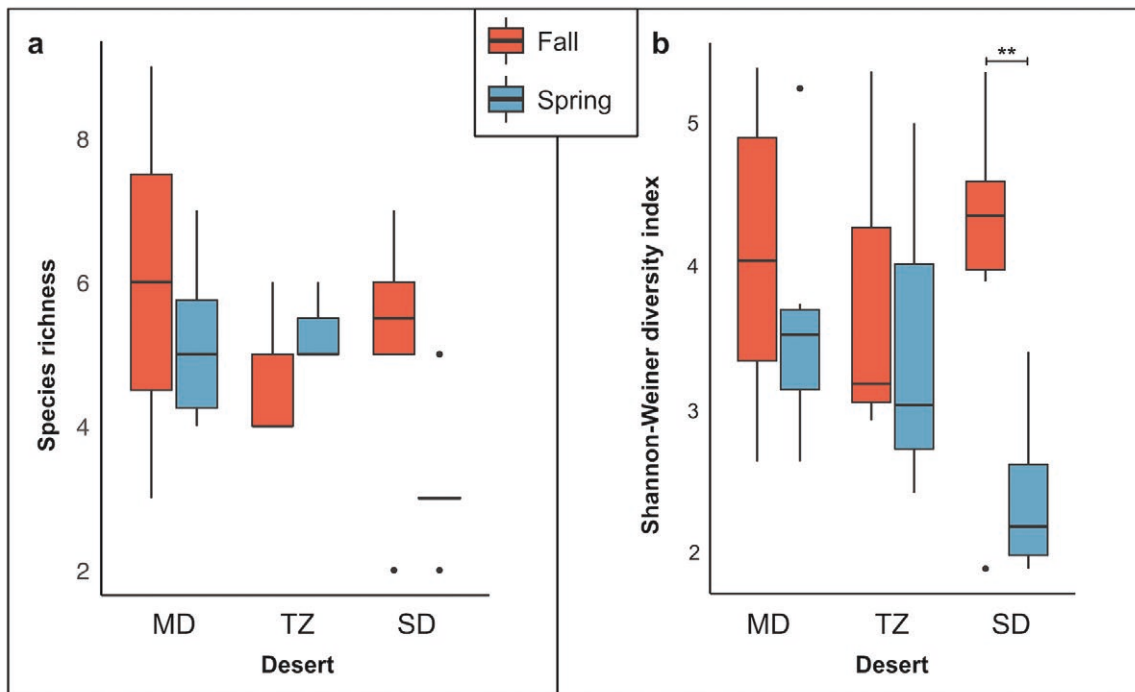


Fig. 3. (a) Species richness within each desert between seasons. Species richness is lower in the TZ and SD in the fall (left bar within desert) relative to the MD. In the spring (right bar within desert), species richness is comparable between the MD and TZ, and relatively low in the SD. No significant differences in species richness were observed across the deserts or seasons. (b) Shannon-Weiner diversity within each desert between seasons. Diversity is comparable between the two deserts in the fall (left bar within desert) and relatively lower in the TZ. In the spring (right bar within desert), diversity decreases along the north-south park gradient. Shannon diversity was significantly lower in the spring only in SD ($P = 0.022$). MD = Mojave Desert, TZ = Transition Zone, and SD = Sonoran Desert.

the BioClim factors are correlated so they had similar loadings, except for mean temperature of the wettest quarter, the mean temperature of the driest quarter, and mean diurnal range. PC2

explained 11.50% of the variation with mean diurnal range, local temperature, temperature annual range, and local relative humidity mainly contributing to PC2.

Table 2. Species richness and Shannon-Weiner diversity of whole park survey

Season	Desert	Site	Richness	Diversity
Fall	Mojave	M1	3	2.64
		M2	4	3.22
		M3	8	5.07
		M4	3	1.95
		M5	6	4.37
		M6	5	3.46
	Transition Zone	T1	4	2.92
		T2	4	3.18
		T3	4	3.39
	Sonoran	S1	2	1.89
		S2	5	3.68
		S3	3	2.37
		S4	3	2.46
		S5	4	3.06
		S6	6	4.68
	Spring	Mojave	M1	4
M2			4	3.03
M3			6	3.58
M4			7	5.24
M5			5	3.74
M6			5	3.47
Transition Zone		T1	6	5.00
		T2	5	3.03
		T3	5	2.42
Sonoran		S1	2	1.89
		S2	3	2.38
		S3	3	1.99
		S4	3	1.98
		S5	3	2.70
		S6	5	3.40

The Mojave desert had the highest species richness, possibly due to a higher number of visitor attractions within this region of the park. Shannon-Weiner diversity was variable throughout the park but higher in the spring season.

Table 3. Results of the Kruskal–Wallis test examining species richness based on visitor activity level (site type) and season

	χ^2	Degrees of freedom	P-value
Site type	1.055	1	0.3
Season	8.943	2	0.011
		Z	P adjusted
Fall—spring		-1.285	0.596
Fall—summer		1.696	0.27
Spring—summer		2.981	0.009

The test revealed no significant difference in species richness between site types. However, there was a significant effect of season on species. Post-hoc pairwise comparisons (using Dunn's test) indicated a significant difference between spring and summer, while other seasonal comparisons were not significant. Significant values are bolded.

Community Composition

There was a significant effect of season and desert on blow fly community composition, but no interaction between season and desert (β dispersion: MD = 0.33, SD = 0.34, TZ = 0.31; NMDS: $R^2 = 0.78$; Stress = 0.20, Fig. 5b, Table 6). A pairwise comparison demonstrated a significant difference between seasons (β dispersion: fall = 0.40, spring = 0.33; PERMANOVA: $F_{1, 29} = 3.87$; $P = 0.003$, Fig. 5b). Pairwise comparisons among deserts demonstrated significant differences between MD and SD ($R^2 = 0.24$; $P_{adj} = 0.003$) and

MD and TZ ($R^2 = 0.22$; $P_{adj} = 0.003$) but not between SD and TZ ($R^2 = 0.06$; $P_{adj} = 1$).

The community composition of collections across 3 seasons at low- and high-visitor activity sites showed no interaction between activity level and season ($F_{2,15} = 0.75$; $P = 0.69$). Though the community composition did not significantly differ between low- and high-visitor activity sites (β dispersion: low = 0.39, high = 0.35; $F_{1,16} = 0.60$; $P = 0.75$, Fig. 6), there was an overall significant difference between seasons without consideration of visitor activity level (β dispersion: fall = 0.18, spring = 0.21, summer = 0.41; $F_{2,15} = 7.49$; $P = 0.001$). Thus, we examined seasonal differences without including visitor activity level as a factor using a pairwise comparison, which revealed significant differences between all seasons (fall vs. spring: $R^2 = 0.45$, $P_{adj} = 0.006$, fall vs. summer: $R^2 = 0.43$, $P_{adj} = 0.009$, spring vs. summer: $R^2 = 0.45$, $P_{adj} = 0.012$).

Indicator Species Analysis

No single species was indicative of each desert region. However, when the analysis was limited by season, *Co. macellaria* was identified as an indicator species for the SD and TZ during fall (stat = 0.92; $P = 0.026$), while *L. sericata* and *Ca. coloradensis* were identified as indicator species for MD and TZ during spring (*L.s.*: stat = 0.96; $P = 0.012$; *C.c.*: stat = 0.92; $P = 0.032$).

When comparing high-visitor activity sites to low-visitor activity sites, there were no overall indicator species recommended. Within sites, *Ca. coloradensis* (stat = 1; $P = 0.038$), *Ca. latifrons* (stat = 0.99; $P = 0.024$), and *Ph. regina* (stat = 0.99; $P = 0.023$) were indicator species for fall and spring at high-visitor activity sites. For low-visitor activity sites, *Ch. rufifacies* was an indicator during the fall season (stat = 0.98; $P = 0.025$), *L. sericata* was an indicator during the spring (stat = 0.97; $P = 0.039$), and *Ca. latifrons* and *Ph. regina* were indicators for the fall and spring (*Ca. latifrons*: stat = 1; $P = 0.039$, *Ph. regina*: stat = 0.99; $P = 0.039$).

Discussion

Blow Fly Community Composition in Neighboring Desert Regions

This study investigated the community structure of blow flies within Joshua Tree National Park to understand how desert environments may shape communities of organisms that rely on ephemeral resources. Results from this study provide a starting point for understanding how ephemeral resource patches act as an environmental filter on regional species pools in desert environments. We find that larger-scale environmental heterogeneity, such as climate and elevation, likely shapes the community assembly of blow flies in desert ecosystems. While community composition varied significantly between the Mojave and Sonoran Deserts, the transition zone exhibited similarities with both, demonstrating the complexity of factors influencing blow fly communities, including surrounding flora and fauna and other unmeasured variables such as carrion resource competitors and park management strategies. Differences in community composition, even on a relatively small spatial scale, provide more support for using the blow fly-carrion system as a potential model system for studying longstanding ecological questions about ephemeral resource patches and how they drive processes of community assembly, especially in harsh environments.

Throughout Joshua Tree National Park, the most abundant species found were *Ph. regina* and *Co. macellaria*. These two species were also the most abundant species found in a similar study in an arid region of Baja California, Mexico (Munguía-Ortega et al. 2021). Similarly, *Co. macellaria* was the most abundant species found in

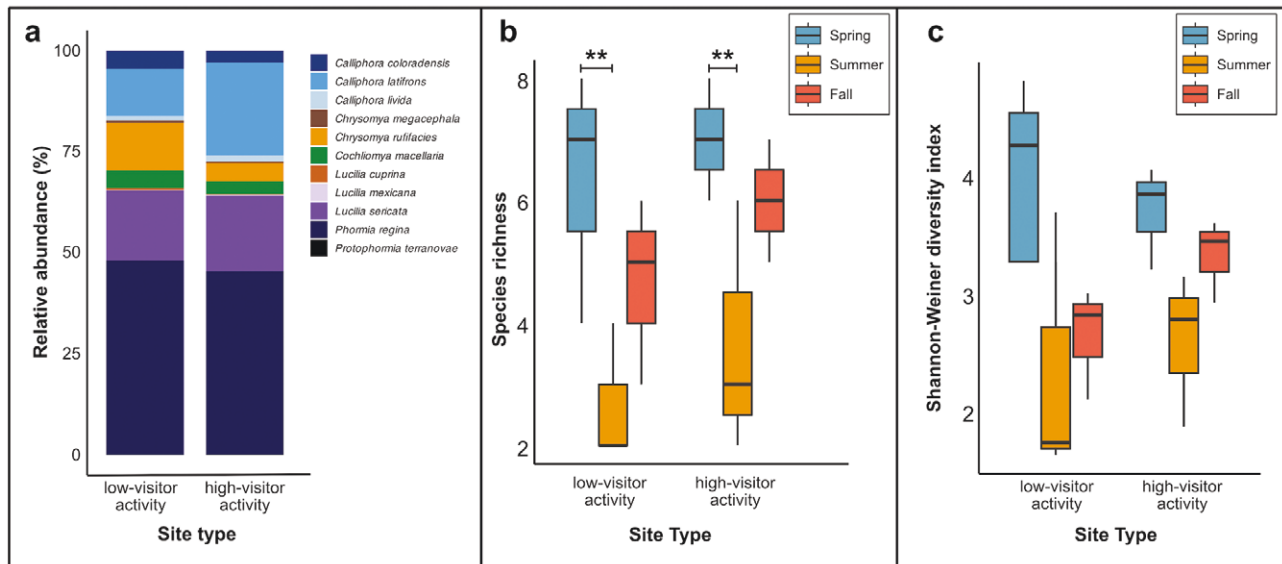


Fig. 4. (a) Relative abundances of blow flies in sites with low-visitor and high-visitor activity. (b) The species richness within each site type among seasons. Species richness was highest in the spring (left bar per site type) and lowest in the summer (middle bar per site type) across both site types. Significant differences between spring and fall (right bar per site type) were observed in both site types ($P=0.009$) (c) Shannon-Weiner diversity within each site type among seasons. The species diversity was also highest in the spring (left bar per site type) and lowest in the summer (middle bar per site type) across both site types. Species diversity was slightly higher at low-visitor activity sites in the spring, but slightly lower in the summer and fall (right bar per site type) relative to the high-visitor activity sites. There were no significant differences between seasons or site types.

Table 4. Species richness and Shannon-Weiner diversity in low-visitor and high-visitor activity trap sites

Season	Type	Site	Richness	Diversity
Fall	High-visitor activity	HV	7	3.62
		RM	6	2.94
		JR	5	3.46
	Low-visitor activity	M2	6	3.02
		M4	5	2.84
		M6	3	2.12
Spring	High-visitor activity	HV	8	3.22
		RM	6	4.07
		JR	7	3.86
	Low-visitor activity	M2	8	4.82
		M4	4	2.3
		M6	7	4.28
Summer	High-visitor activity	HV	3	2.8
		RM	2	1.89
		JR	6	3.16
	Low-visitor activity	M2	4	3.71
		M4	2	1.65
		M6	2	1.75

Species richness and Shannon-Weiner diversity were highest in the spring, but comparable between high- and low-visitor activity sites.

HV = Hidden Valley Campground; RM = Ryan Mountain Campground; JR = Jumbo Rocks Campground; M = Mojave Desert.

the Chihuahuan Desert (Schoenly and Reid 1983) and the Mojave Desert (Cumming and Dufek 2021). Records of *Pr. terraenovae* have not been previously published in southern California. *Protophormia terraenovae* is considered a high-elevation species, so it was not surprising to find this species at JOTR's elevation (specimen collected at Hidden Valley Campground: 1283 m) (Adair 1999, Adair and Kondratieff 2006, Jones et al. 2019). The remaining 10 species collected during this study have been previously reported in southern California, with the most recent records from Los Angeles (LA)

County, ca. 245 km west of the park (James 1955, Cumming and Dufek 2021). In the LA County study, traps designed by the first author were baited with 100 g of 2:1 beef:chicken liver and left out for 48 h (Cumming and Dufek 2021). Across 10 sampling events, only 61 individuals were collected from the Mojave Desert, a similar region from this study, representing the lowest abundance of blow flies relative to urban and coastal mountain ecoregion collections (Cumming and Dufek 2021). These results suggest that there are likely community differences based on bait and trap type which has been demonstrated in previous studies (e.g., Moretti and Godoy 2013, Vasconcelos et al. 2015, Leblanc et al. 2021, Façanha et al. 2022) but also that the squid bait may be more attractive to desert populations of blow flies, or attractive for longer periods of time. In our study, traps were only deployed for 4–5 h. One study examined spatio-temporal variability in preference for bait type in calliphorid flies and found that all calliphorid species preferred chicken gizzards (Moretti and Godoy 2013). However, this study was conducted in a subtropical region of Brazil, which may indicate that the preference for squid bait in the current study might be related to a drier climate as suggested by previous work (Baz et al. 2013, Brett et al. 2021). This warrants further study on differences in resource preference of locally adapted blow fly populations at a larger spatial scale.

In this study, elevation did not have a significant effect on species richness nor α -diversity. This was surprising as other studies have found that arthropod species richness tends to increase with elevation; however, these studies were conducted over a smaller spatial scale as opposed to this study that had comparable elevation ranges (531–1,428 m) over a much larger spatial scale (Sanders et al. 2003, Flores et al. 2018, Supriya et al. 2019, Pilar et al. 2020). It is possible that the sampling frequency or location of the present study failed to capture elevation differences. Interestingly, communities of flora and fauna within the park are generally more diverse in the lower elevation Sonoran Desert (Sponseller et al. 2012, Fraga et al. 2023). A faunal study of aculeate wasps in JOTR found that diversity increased with decreasing latitude, presumably due to higher

Table 5. Numbers and percentages of non-native (*Ch. spp.*) versus native species in high- and low-visitor activity sites

Site	Fall				Spring				Summer				
	Non-native spp.	Native spp.	Total	Non-native percentage	Non-native spp.	Native spp.	Total	Non-native percentage	Non-native spp.	Native spp.	Total	Non-native percentage	
High-visitor activity	HV	36	68	104	34.6	0	453	453	0	0	10	10	0
	JR	9	23	32	28.1	1	298	299	0.33	6	28	34	17.65
	RM	1	42	43	2.3	0	127	127	0	0	3	3	0
Low-visitor activity	M2	46	75	121	38.0	3	232	235	1.28	2	7	9	22.22
	M4	14	36	50	28.0	0	166	166	0	0	5	5	0
	M6	18	9	27	66.7	0	64	64	0	2	6	8	25

The percentage of non-native flies was relatively higher in the low-visitor activity sites in the fall, but low in both the spring and summer. The abundance of native flies was high in the spring and very low in the summer, likely due to higher temperatures in the summer.

HV = Hidden Valley Campground; RM = Ryan Mountain Campground; JR = Jumbo Rocks Campground; M = Mojave Desert.

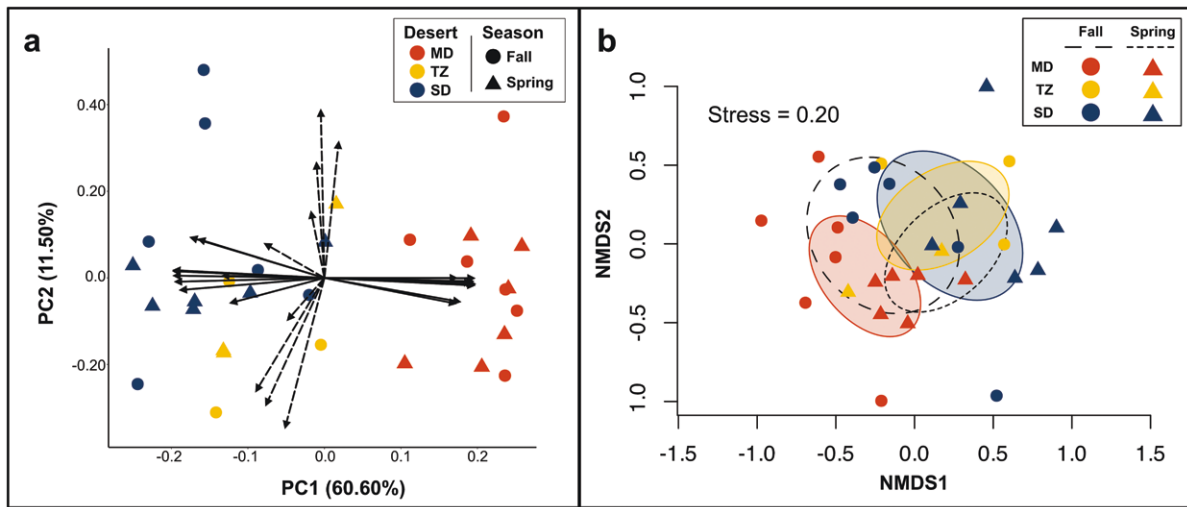


Fig. 5. Environmental PCA and NMDS of community composition in each desert (a) Environmental PCA where PC1 explains 60.60% of variation and PC2 explains 11.50% of variation. Dotted lines indicate locally measured variables. Climate variables separated out into PC1 and local environment variables are described by PC2. (b) NMDS (Stress = 0.20) of overall park survey across season. SD and TZ significantly overlap. Circles indicate the Fall season and triangles indicate the Spring season.

Table 6. PERMANOVA analysis examining the effects of Desert, Season, and their interaction on community composition

	Degrees of freedom	Sum of squares	F-value	R ²	P-value
Desert	2	1.742	5.392	0.251	0.001
Season	1	0.843	5.218	0.121	0.001
Desert:Season	2	0.478	1.48	0.069	0.126
Residual	24	3.878		0.559	
Total	29	6.941		1	

The model demonstrates that both Desert and Season have significant effects on species composition. However, the interaction between Desert and Season was not significant. Significant values are bolded.

diversity and abundance of insects they can parasitize (Sadler et al. 2018). In this study, species diversity was only observed between seasons. This may suggest that blow fly diversity is not heavily influenced by biotic factors, such as the desert environment (including vegetation), but rather by abiotic factors, such as seasonal climatic differences.

To identify differences in community composition between deserts, we first examined the established desert ecoregions based solely on environmental data. The environmental analysis showed that each desert ecoregion significantly differed from one another,

though the transition zone was more similar to the Sonoran Desert, which was reflected by our community data. This suggests that environmental heterogeneity heavily influences blow fly community assembly processes, even though carrion is a prime example of a resource that would promote pure dispersal assembly. In deserts, the environment may play a more important role relative to resource availability in community assembly. Previous studies have noted that the drivers of β -diversity in arthropod communities highly vary, with some studies demonstrating that while spatial signatures remain in community assembly patterns, regional environmental filtering and

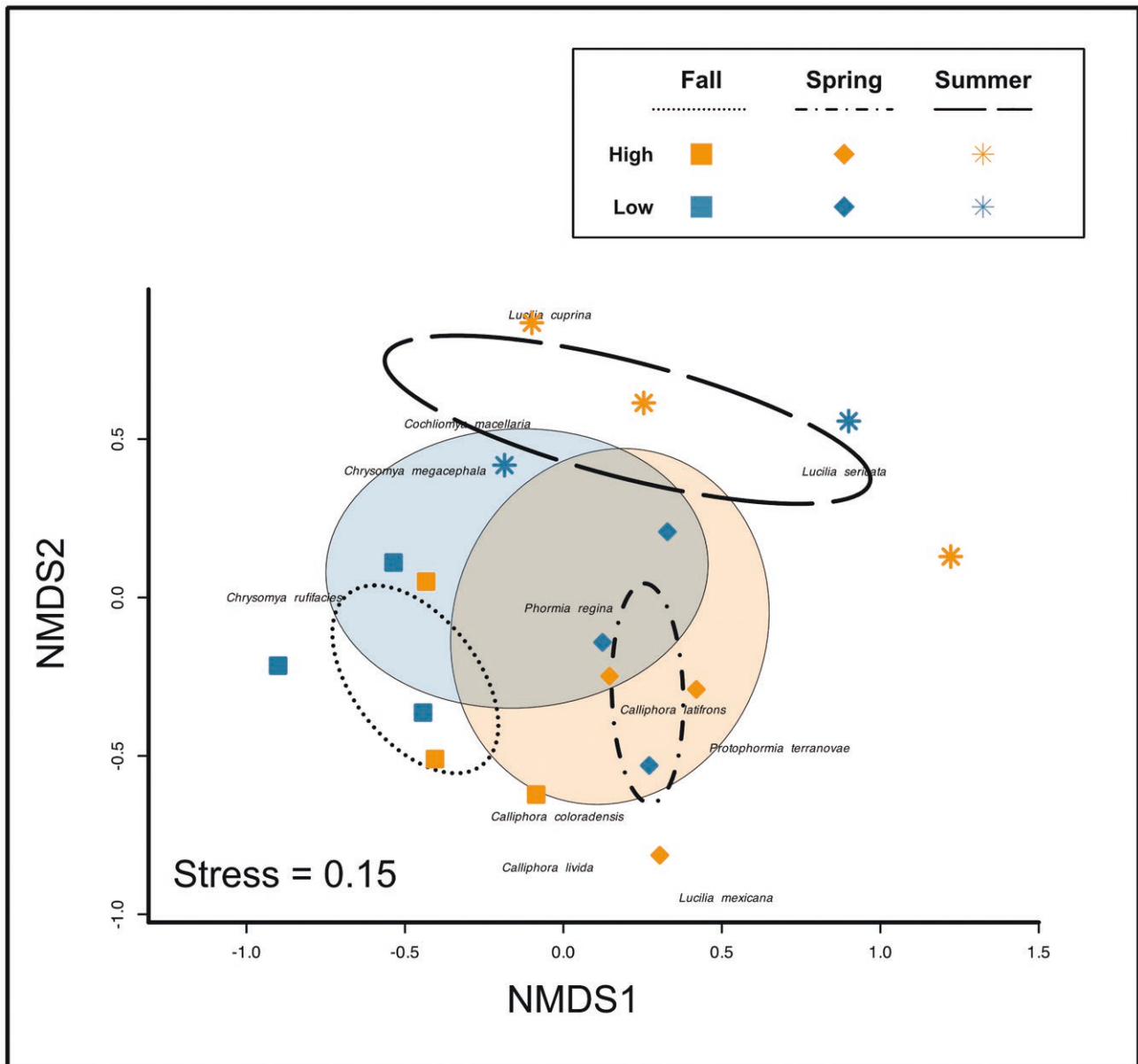


Fig. 6. NMDS of low-visitor and high-visitor activity sites across season (Stress = 0.15). There is great overlap between low- and high-visitor activity level sites, but clear seasonal separation. Squares/dotted lines = Fall, Diamonds/short dashed lines = Spring, Stars/long dashed lines = Summer.

insect dispersal ability supersede local factors in determining regional species pool (Bacca et al. 2021, Grigoropoulou et al. 2022). Other studies show that β -diversity is primarily driven by geographic distance, followed by bioclimatic variables (McCreadie and Adler 2018, Chesters et al. 2019). These contrasting findings demonstrate that patterns in community assembly are highly system specific, in which more research would help parse out traits associated with β -diversity patterns that arise. While we expected to find indicator species that could characterize each region, we did not find any indicator species that were unique to each desert. This suggests that while there were significant differences in community composition, these differences were not driven by a single species.

Impact of Human Activity on Blow Fly Communities Within JOTR

With recent suggestions that blow flies could be ideal indicators of human activity level (Dufek et al. 2021), we were interested to see

whether this could be measured at small scales within conserved areas, like national parks. We expected to see lower species richness and α -diversity in low-visitor activity sites because of unpredictable resource availability; however, we found that these two metrics did not differ between high-visitor and low-visitor activity sites. Previous studies on urban–rural gradients on a larger scale have conflicting results, with some showing a higher abundance of blow flies in rural/natural areas (e.g., Moretti and Godoy 2013: forest sites, Langer et al. 2019: agricultural, semirural, and wilderness landcover) and others finding a higher abundance of blow flies in urban areas (e.g., Babcock et al. 2020, Cumming and Dufek 2021). Studies that found a higher abundance of flies in their traps in rural areas propose that there may have been an abundance of other resources that flies may have been attracted to colonize, though this was not tested (Moretti and Godoy 2013).

Though abundance was almost double in high-visitor activity sites compared to low-visitor sites, this result was not statistically significant, suggesting that resource predictability may influence

abundance, but not richness nor diversity. Ephemeral resources, like carrion, can shape fly abundance captured in baited traps as the availability of background resources likely interacts with the attractiveness of these traps in complex ways. In an environment with high background resource availability, flies may be less drawn to traps. Alternatively, high resource availability may lead to increased fly reproduction, resulting in a larger overall population and consequently higher trap abundance. Both scenarios have different temporal considerations, with the former accounting for the adult flies occupied by current abundant resources, and the latter explaining the already depleted resources by the immature stages with large numbers of “new” adults seeking a resource. These complex interactions and overall trap efficacy are not well known in this system. Ultimately, the influence of background resource availability on the efficacy of baited traps warrants further study.

Another pattern that has been observed in the increasing association of blow flies with human activity is the spread of non-native blow fly species, such as *Ch. rufifacies* and *Ch. megacephala* (Dufek et al. 2021, Langer et al. 2019, Cumming and Dufek 2021). Therefore, we examined the ratio of non-native species counts relative to native species counts. Previous studies have reported higher numbers of non-native species in urban environments with higher levels of human disturbance (Dufek et al. 2021, Langer et al. 2019). In our study, we found that non-native species, though less abundant overall, were relatively more prevalent in low-visitor activity sites. Although this result was not statistically significant, it suggests that waste management practices at high-visitor activity sites, like campgrounds, may impact the success of non-native species, which are considered secondary colonizers in the United States (Baumgartner 1993) in the park. Following Odum's niche-based assembly theory (1969) and Connell and Slayter's facilitation model (1977), secondary colonizers prefer to colonize a resource only after a “pioneer” colonizer has already arrived. This is likely because primary colonizers have already begun the exodigestion process, allowing secondary colonizers to reduce metabolic energy (Wells and Greenberg 1994, Shiao and Yeh 2008, Galindo et al. 2016, Carmo et al. 2018). Human-generated waste at these sites might provide sufficient resources for pioneer colonizers to develop into adults, but the regular removal of waste likely disrupts the full development cycle of secondary colonizers (non-native species). In contrast, at low-visitor activity sites where waste and carrion are not removed, secondary colonizers can complete their development.

The observational nature of this study limits our ability to draw direct conclusions about the impacts of human activity and vegetation. Future studies may consider longer sampling periods as this study only spanned 2 yr. Additionally, more sites could be added that are farther away from roads in designated ‘wilderness’ areas. This study provides the first list of species records for JOTR. Though desert ecosystems are harsh, our results suggest that blow fly communities are consistent and influenced by long-term patterns, such as climate, and not daily environmental fluctuations. Continued monitoring will not only expand this dataset and enhance our understanding of blow fly resource use in deserts but will also provide up-to-date information on species presence in the park.

Supplementary data

Supplementary data are available at *Environmental Entomology* online.

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Author contributions

Hannah Chu (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Funding acquisition [equal], Methodology [equal], Project administration [equal], Resources [equal], Visualization [lead], Writing—original draft [lead], Writing—review & editing [equal]), and Amy Murillo (Conceptualization [equal], Funding acquisition [equal], Methodology [equal], Project administration [equal], Resources [equal], Supervision [lead], Writing—review & editing [equal])

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