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The Impact of Roads on the Redistribution of Plants and Associated Arthropods in a Hyper-Arid Ecosystem

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Abstract

The construction of vehicular roads likely affects the distribution of natural resources. Although the effects of roads on different ecosystem aspects have been extensively studied, studies in arid and, particularly, in hyper-arid ecosystems are scarce. In drylands, where water is the main limiting factor, the effect of roads on the redistribution of water may have strong subsequent effects on the ecosystem, especially when roads cross natural water flow paths. To fill this knowledge gap, we studied the effects of a road that runs across a slope on the distribution of plants and animals in a hyper-arid environment. Changes in shrub cover, below and above the road, were quantified by remote sensing and image classification, while plant-associated arthropods were vacuum-sampled from shrub canopies and from open (inter-shrub) areas. We found that the spatial distribution of shrubs, a vital resource facilitating many other organisms, was affected by the road, with an increase in the shrub cover immediately above the road and a decrease below it. Arthropod abundance generally followed shrub cover, but the exact pattern depended on the specific group sampled. While some arthropod groups (e.g., aphids, parasitic wasps and barklice) thrived under the disturbed conditions above the road, other arthropod groups (e.g., mites and true bugs) were less abundant in the disturbed patches. Our results highlight the strong effects of human-made structures on the distribution of flora and fauna in arid ecosystems.

Key words: road zone, arthropods, community ecology, disturbances, hyper-arid

Human activities affect the environment, notably through the spatial redistribution of resources (Vitousek et al. 1997, Kosmas et al. 1997, Forman and Alexander 1998, Alberti 2005, García-Ruiz 2010, Zhuang 2016). One important example of this is the construction and maintenance of human-made structures, leading to the accumulation of resources in specific areas, with the structure acting as a barrier and preventing resource flow downstream. Resource redistribution may cause changes in not only the spatial distribution of plant and animal species, but also their population densities and diversity, as well as in ecosystem structure and function (Lightfoot and Whitford 1991, Forman and Alexander 1998, Jones et al. 2000, Duniway and Herrick 2011).

The ecological impacts of vehicular roads have been extensively studied, mostly in temperate environments, and may include habitat loss, habitat fragmentation, habitat degradation, barrier effects, light, noise and chemical pollution, and direct mortality due to road kills or electrocution from road-related infrastructure (e.g., Forman et al. 2003, Coffin 2007, Tamayo-Muñoz et al. 2015, Ouédraogo et al. 2020). In addition, roads are known as a common factor in the disruption of the natural spatial distribution of resources, particularly water (King and Tennyson 1984, Lamont et al. 1994, Donaldson and Bennett 2004, Duniway and Herrick 2011). Because of their heavily compacted surfaces, roads tend to generate runoff water and to divert subsurface flow onto the surface (King and Tennysson 1984, Jones et al. 2000). As artificial networks, roads often do not follow gravitational flow channels, such as slopes or streams, but instead, run across them (Jones et al. 2000). A road that cuts through a slope often functions as a barrier to horizontal flows in the landscape, causing asymmetrical effects on the two road sides (Forman and Alexander 1998, Forman 2000, Brooks and Lair 2005, Andersen 2007). In cases in which the road surface is more elevated than the natural surface, there is often an increase in the soil water content upslope from the road, and around its drainage trenches (Brooks and Lair 2005, Andersen 2007), at the expense of downslope areas (Luce 2002, Duniway and Herrick 2011, Waddell et al. 2012). This may cause an increase in the vegetation density and vigor above the road, while simultaneously reducing it downstream from the road (Lightfoot and Whitford 1991, Forman and Alexander 1998, Forman 1999). Moreover, the accumulation of water near roads, in combination with gas emissions from vehicles, may cause an increase in nitrogen concentrations in roadside vegetation (Kammerbauer and Dick 2000), thereby increasing the palatability of the leaf tissues for some herbivore arthropods (e.g., Heteroptera; Spencer et al. 1988).

The effect of roads may be particularly pronounced in water-limited ecosystems. In drylands, the disruption to the natural distribution of water resources may have significant effects on the ecosystem, at various scales. Due to the low water infiltration rates of many desert soils, or the lack of soils in some areas, overland flow (runoff) is a major contributor to water distribution and to the regulation of productivity in these ecosystems (Noy-Meir 1973, Shmida et al. 1986). The typical arrangement of shrubs in water-limited ecosystems forms a two-phase mosaic landscape, which consists of shrub patches within a matrix of bare ground, with some herbaceous vegetation and biogenic soil crust (Shachak et al. 1998, Montaña et al. 2001). Water runoff is produced in the bare inter-shrub area (hereafter "open" patches), from where it flows to sink in the evenly distributed shrub patches, providing water, nutrients and dispersal pathways, which enable the facilitation of many dryland organisms. (Shachak et al. 1998, Yu et al. 2008). The continuous pattern regulates the erosive properties of runoff fluxes, as well as the harsh environmental conditions in drylands by providing vital resources. The open patch provides a significant seasonal input of lichens, seeds, pollen, and other plant products with high nutritional importance for many arthropods, making these patches important habitats for desert communities (Shelef and Groner 2011, Wasserstrom et al. 2016, Liu and Steinberger 2018).

Following water redistribution, the spatial distribution of shrubs may undergo major state shifts (Zelnik et al. 2016, Bresheárs et al. 2016, Hoffman et al. 2017), which may include changes in the relative shrub area in relation to the relative open patch area. Such changes may launch a positive feedback, causing a possible runoff-driven loss of resources (Mayor et al. 2019), which may subsequently affect the productivity and diversity of plants and animals in the disturbed areas (Spencer et al. 1988, Lightfoot and Whitford 1991, Lamont et al. 1994, Donaldson and Bennett 2004).

While the impact of roads in arid ecosystems has been studied to some extent (e.g., Brooks and Lair 2005, Raiter et al. 2018), very little work has been done in hyper-arid areas (i.e., with an aridity index of less than 5%, Geiger 1961, Atlas 1992). Hyper-arid ecosystems differ substantially from other arid systems in their hydrology and vegetation distribution (Saco et al. 2007, Dahan et al. 2008). In comparison with other, less arid, dryland environments, in which vegetation is distributed on plains and slopes, vegetation in hyper-arid environments is mostly concentrated in watershed's topographically lowest parts and in the river beds of ephemeral streams (called "wadis" in Arabic), which receive the majority of the water resources in these runoff-driven ecosystems (Shmida 1985, Fossati et al. 1998). Hence, disturbances to the water flow in the wadis may cause major cascading effects.

To fill this knowledge gap, in this study, we examined the effect of a vehicular road that runs across a slope and intersects a wadi system on plant and animal distribution in a hyper-arid ecosystem. We used remote sensing in order to characterize variations in the spatial distribution of the shrub patches in relation to the road. We used arthropods as bioindicators in the assessment, due to their high diversity and high sensitivity to environmental changes (Kremen et al. 1993, Carignan and Villard 2002). To this end, we characterized the abundance and composition of the assemblages of plant-associated arthropods, upstream and downstream from the road. The term "plant-associated arthropods" is a generalization that encompasses arthropods that inhabit the above-ground plant environment (Utsumi 2013, Ando et al. 2017, Harrison et al. 2018). They exploit a wide range of ecological niches and feeding behaviors and are often sensitive to spatial heterogeneity, environmental fluctuations, and disturbances (Brown Jr 1991, Kremen 1992, Kremen et al. 1993). Disruptions to resource distribution may have different impacts on the different species in the assemblage due to the various dispersal mechanisms and their abilities to cope with the changing conditions. These various characteristics may eventually cause shifts in the arthropod assemblages' abundance and composition following disturbances.

Based on the above, we hypothesized that the road functions as a barrier to the runoff fluxes, affecting shrub cover and spatial distribution. We further hypothesized that this has an impact on the quantity of food resources for the plant-associated arthropod assemblages, causing shifts in their abundance and composition.

Methods

Study Site

The field work took place during spring 2016 in the Ramon Crater LTER (Long Term Ecological Research) site (Negev Desert, Israel, https://deims.org/52d25867-33e7-4f27-8e0c-4f8a74bf22e0). This is a hyper-arid region with mean annual rainfall of 50 mm (IMS, www.ims.gov.il). The elevation of the study site is 485–515 m above sea level. This area was previously dominated by quarrying operations and includes an old dirt access road that runs through the slope, cutting across a series of small wadis. After the quarrying operations ceased (in 2000), the road was improved with an imported gravel fill; it now serves as a scenic road (https://www.parks.org.il/wp-content/uploads/2017/08/ramonShaar.pdf). The road seems to function as a barrier to the horizontal water flows in the system, providing an opportunity to study the effect of water redistribution on this fragile ecosystem. The area is characterized by a two-phase mosaic of shrub patches and open patches with no shrubs, but with some annual plants. The dominant shrubs in the area are *Haloxylon salicornicum* (Moq.) Bunge ex Boiss, *Zygophyllum dumosum* Boiss., *Salsola vermiculata* L., and *Zilla spinose* L. There are no trees in the study area.

Study Design

Ten wadis that intersect the road were chosen, and four plots were sampled in each wadi (Fig. 1). Upstream plots (U) were located immediately above the road. These plots were likely to be directly affected by the road, as water and, consequently, vegetation tend to accumulate in this area. Downstream plots (D) were located immediately below the road. These were also likely to be directly affected by the road, due to the immediate limitation of water input. Further upstream plots (FU) were located ~50 m upstream from the road, and further downstream plots (FD) were located ~50 m downstream from the road. These plots (and especially the FU plots) were less likely to be directly affected by the road and, therefore, were considered as comparably less disturbed plots.

Shrub Cover

In order to examine the effects on the spatial distribution of the shrub cover, the relative area covered by shrubs was evaluated in each plot, using a process that was based on input from remotely sensed imagery. For computing the relative shrub cover area, rectangular plots of ~1624 m^2 (fixed length of 77.63 m and mean width of 20.92 m) were defined. The plots were selected at 10 locations where the wadis cross the road, above and below the road (Fig. 1).

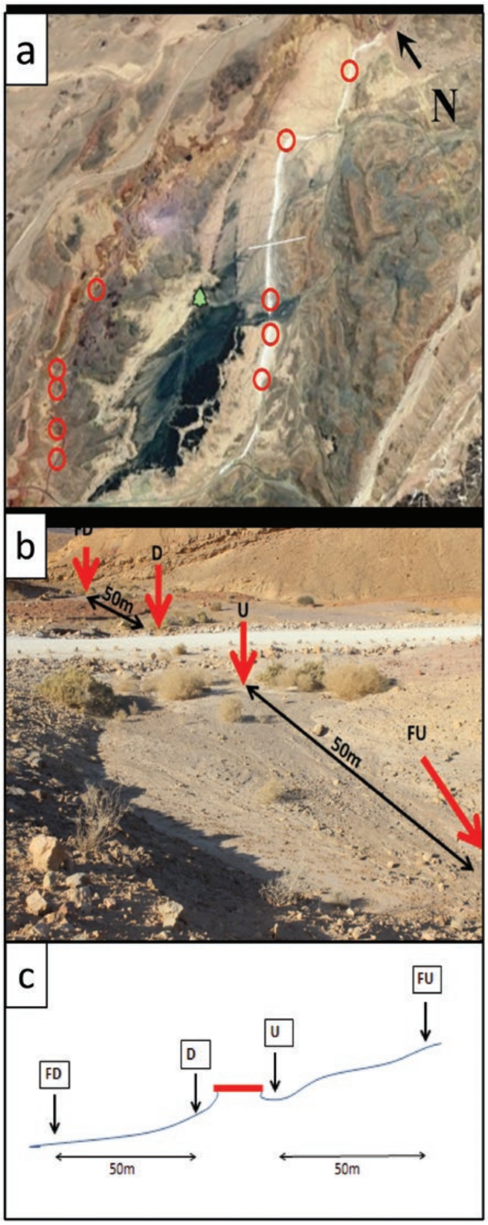

Fig. 1. (a) An overview of the field site in the Ramon crater, Israel. The circles indicate the location of the 10 wadis that intersect the road that were sampled in the study. (b) An upper view of the sampling site. The arrows indicate the locations of the different plots sampled along the wadi. U: upstream (immediately above the road), D: downstream (immediately below the road), FU: further upstream (~50 m above the road), and FD: further downstream (~50 m below the road). (c) An illustration of a side view of a wadi. The black arrows indicate the relative locations of the various plots and the red line marks the location in which the road cuts through the wadi.

The first step consisted of using a multispectral image with a spatial resolution of 15 cm, which was acquired with a UAV in May 2017 (imagery source, Terrascan Labs Ltd.). The image was used to extract the Normalized Difference Vegetation Index (NDVI) (Kriegler et al. 1969, Rouse et al. 1973).

However, due to water-stressed conditions, hyper-arid areas often exhibit very low NDVI values, which resemble the NDVI values of bare soil and rocks (maximum NDVI value in the study area is 0.429). This, combined with the variability of the geology and soil cover that characterize the Ramon Crater, resulted in areas where shrubs were omitted from the recognition (Fig. 2a). To account for the omitted vegetation, an RGB (red, green, and blue) image was produced from the multispectral UAV image with a spatial resolution of 15 cm. An unsupervised classification method that combined an ISODATA clustering algorithm (Ball and Hall 1965) with the maximum likelihood (ML) classification method was applied in ArcGIS PRO (ESRI 2017) to recognize vegetation patches. Outputs were combined with the outputs of the NDVI-based recognition. The final output consisted of an image in which each pixel was defined as "with plants" or "without plants." Pixels representing plants were vectorized to define the vegetation patch boundaries (Fig. 2b), and the total shrub area within each upstream and downstream plot was calculated. This was used to examine the effect of plot type (location relative to the road) on the vegetation cover area.

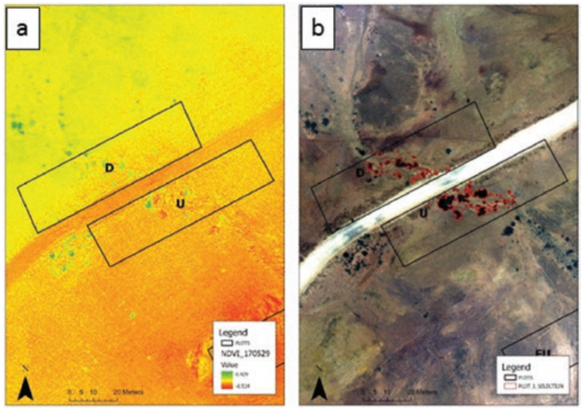

Fig. 2. (a) Vegetation patches in the NDVI image (green) are partly omitted, mainly within plot U, and appear instead as red patches, due to the low NDVI values of hyper-arid vegetation, which resembles bare soil and rocks. These patches are clearly visible in the RGB image (b). (b) Final outputs combining NDVI-based recognition of vegetation patches with RGB-based clustering, focusing on two plots adjacent to the path. Red polygons represent the boundaries of recognized vegetation patches overlaid on the RGB orthophoto.

Arthropod Assemblage

Within each plot (FU, U, D, and FD), two patch types were sampled (shrub patch and open patch). Shrub patches included arthropods present on the shrub canopies, and open patches included arthropods on the inter-shrub annual vegetation. Altogether, 80 points (2 patch types × 4 plots × 10 wadis) were sampled for plant-associated arthropods.

From each of the sampling points, plant-associated arthropods were sampled either from shrub canopies (in the shrub patches) or from annuals (in the open patches) using a Vortis insect suction sampler (http://www.burkard.co.uk/vortis.htm). This device allows even the smallest arthropods to be captured with minimal damage (Borges and Brown 2003, Cherrill 2015). Each sampling was performed for a 30-s period, covering an area of ~4^2 m. The sampling of the shrub patches was done almost exclusively from the canopies of *Haloxylon salicornicum* (Moq.) Bunge ex Boiss, which were present in all the sampled plots. The sampled material was deposited into a container with ethanol and kept cool until sorting and identification. Arthropods were identified to the subclass, order, sub-order, or family taxonomic level, from which some unifying traits (e.g., movement abilities, preferred habitats, and diet) could be used to explain the assemblage turnover, under varying environmental conditions.

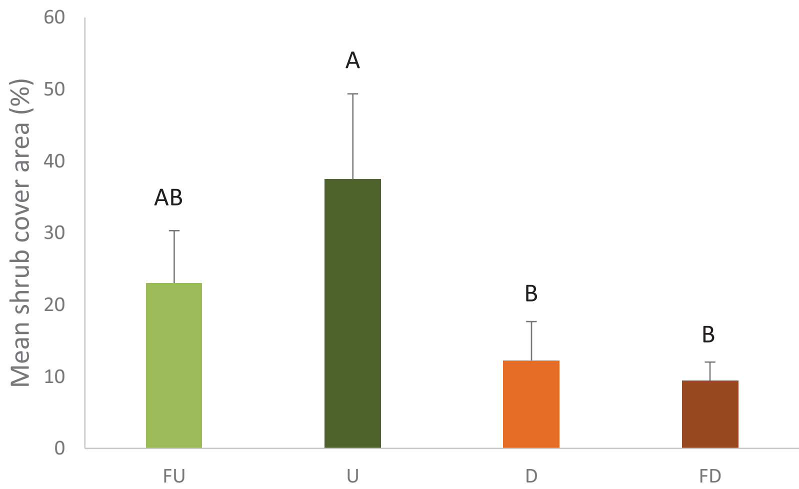

Fig. 3. Mean (±S.E.) shrub cover in the various plot types (location in relation to the road) in the Ramon study area. U: upstream (immediately above the road), D: downstream (immediately below the road), FU: further upstream (~50 m above the road), and FD: further downstream (~50 m below the road).

Data Analysis

To examine the effect of plot type (location in relation to the road) on the relative shrub cover area, we used univariate ANOVA tests. The Bonferroni method was used for post hoc comparisons. To examine the effect of plot type (location in relation to the road) and patch type (shrub vs. open) on the abundances of the different arthropod groups, we used a GLMM (generalized linear mixed models) test, with a Poisson probability distribution and a log-link function, with total arthropod abundance, or the abundance of a specific arthropod group, as response variable, "plot type" (U, D, FU, and FD) and "patch type" (shrub vs. open) as fixed factors, and the wadi identity as a random factor. The interaction between the fixed factors was also included, so DF was calculated according to the number of levels in each factor (*N*–1). Since the analyses were conducted for each group separately and the number of comparisons was not large, post hoc comparisons were conducted using the sequential Holm–Bonferroni method (Kim 2015, Giacalone et al. 2018). The likelihood-ratio χ^2 was computed to interpret the significance of each model, and residuals were tested for normality and homoscedasticity. All of the tests were conducted in the SPSS V24 software (IBM Corp, 2016).

Partially constrained ordinations were performed in order to characterize the variability in the species composition data that could be explained by the measurable environmental variables (plot type, patch type, and their interaction) (Verdonschot and Ter Braak 1994, Šmilauer and Lepš 2014). Since a DCA test (Detrended Constrained Analysis) revealed a relatively homogeneous data set (1.6 SD), a partial RDA (Redundancy Detrended Analysis) test was selected, assuming a linear response (Šmilauer and Lepš 2014). The response data (abundance of taxa) were log-transformed and standardized by species center (subtraction of the means so that the resulting variable has the mean of zero; Šmilauer and Lepš 2014). In order to express the sampling design, the plot (wadi) identity was defined as a covariable, and blocks for permutations were defined by the covariables. Four models were constructed: an unconstrained model and three partially constrained models (with the plot type, the patch type, and their interaction as three separate models). For each model, 999 permutations were conducted. All the ordination tests were conducted using the software CANOCO 5 (http://www.canoco5.com).

Results

Relative Shrub Cover

Based on the univariate ANOVA tests, it can be seen that plot location, in relation to the road, had a marginally significant effect on shrub cover (one-way ANOVA $F_{3,36}$ = 2.802, P = 0.054; Fig. 3). Post hoc tests revealed significantly higher shrub cover immediately above the road (U plots), where water often accumulates, than in the plots below the road (D and FD), while the shrub cover in the far upstream plot (FU) was intermediate.

Arthropod Abundance and Composition

In total, 10,747 individual arthropods were collected. The most common groups of plant-associated arthropods were mites (Acari; 23.6% of the total catch), thrips (Thysanoptera; 20.2%), aphids (Aphidoidea; 20.1%), parasitic Hymenoptera (10.1%), Psocoptera (8%), and Heteroptera (5.3%; Fig. 4).

Plot type, patch type, and the interaction between them all had significant effects on total arthropod abundance (Table 1; Fig. 5). Arthropod mean abundance was higher in the plots above the road (U and FU) than in those below the road (D and FD), and the differences were significant even between the U and D plots, which were only ~10 m apart. However, the pattern differed between patch types: in the open patches, arthropod abundance was highest in the far upstream plot (FU), while in the shrub patches, it was highest in the plot immediately above the road (U). In general, the differences between the plots were more pronounced in the open than in the shrub patches, and the contrast between the patch types was most pronounced in the FU plot (Fig. 5).

Plot type, patch type, and the interaction between them differed in their effects on the different taxonomic groups (Table 1; Fig. 6). Focusing on the six most abundant groups, we found that Acari abundance was generally higher in the upper plots (FU and U) than in the plots below the road (D and FD), and was much higher in the open than in the shrub patches, especially in the FU plots (Table 1; Fig. 6a). Thysanoptera abundance was affected by the patch type, being higher in the open patches, especially in the FU and D plots (Table 1; Fig. 6b). Aphidoidea were more abundant in the shrub than in the open patches, particularly, in the U plots (Table 1; Fig. 6c). Parasitic Hymenoptera was more abundant in the shrub patches, particularly, in the U plot. However, in the FU plots, the trend was the opposite, and the abundance was higher in the open patches (Table 1; Fig. 6d). Psocoptera abundance was higher in the open patches than in the shrub patches, and this contrast was most pronounced in the U plots. Psocoptera were almost absent from the shrub patches below the road (Table 1; Fig. 6e). Finally, Heteroptera abundance was highest in the open

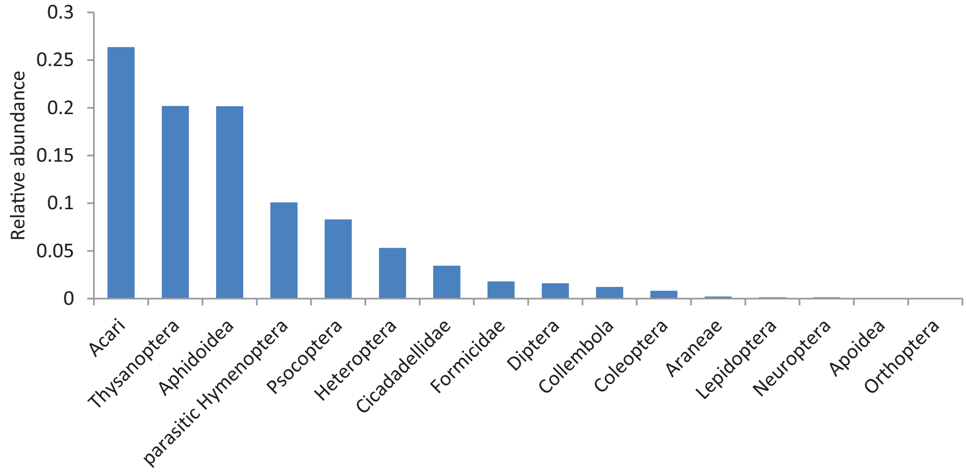

Fig. 4. Relative abundance of plant-associated arthropods sampled throughout the study.

Table 1. GLMM test results, examining the effects of plot types (location in relation to the road), patch types (shrub vs open), and the interaction between them, with the wadi as a random factor, on the abundance of various plant-associated arthropod groups in the Ramon study area

Taxonomic group	Wadi identity	Plot type (location in relation to the road)	Patch type (shrub vs open)	Plot*Patch type
	Random effect	Fixed effect	Fixed effect	Fixed effect
Total abundance	$\chi^2_{(1)} = 0.621$ $P = 0.431$	$\chi^2_{(3)} = 1006.196$ $\mathbf{P < 0.001}$	$\chi^2_{(1)} = 514.166$ $\mathbf{P < 0.001}$	$\chi^2_{(3)} = 604.389$ $\mathbf{P < 0.001}$
Acari (mites)	$\chi^2_{(1)} = 1837.166$ $\mathbf{P < 0.001}$	$\chi^2_{(3)}=153.416$ $\mathbf{P < 0.001}$	$\chi^2_{(1)}=649.318$ $\mathbf{P < 0.001}$	$\chi^2_{(3)} = 381.509$ $\mathbf{P < 0.001}$
Thysanoptera (thrips)	$\chi^2_{(1)} = 342.657$ $\mathbf{P < 0.001}$	$\chi^2_{(3)} = 83.246$ $\mathbf{P < 0.001}$	$\chi^2_{(1)} = 80.881$ $\mathbf{P < 0.001}$	$\chi^2_{(3)} = 48.609$ $\mathbf{P < 0.001}$
Aphidoidea	$\chi^2_{(1)} = 298.369$ $\mathbf{P < 0.001}$	$\chi^2_{(3)} = 175.378$ $\mathbf{P < 0.001}$	$\chi^2_{(1)} = 51.264$ $\mathbf{P < 0.001}$	$\chi^2_{(3)} = 35.662$ $\mathbf{P < 0.001}$
Parasitic Hymenoptera (parasitoid wasps)	$\chi^2_{(1)} = 121.050$ $\mathbf{P < 0.001}$	$\chi^2_{(3)} = 65.153$ $\mathbf{P < 0.001}$	$\chi^2_{(1)} = 25.821$ $\mathbf{P < 0.001}$	$\chi^2_{(3)} = 113.090$ $\mathbf{P < 0.001}$
Psocoptera (psocids)	$\chi^2_{(1)} = 193.429$ $\mathbf{P < 0.001}$	$\chi^2_{(3)} = 201.756$ $\mathbf{P < 0.001}$	$\chi^2_{(1)} = 153.355$ $\mathbf{P < 0.001}$	$\chi^2_{(2)} = 7.880$ $\mathbf{P < 0.05}$
Heteroptera (true bugs)	$\chi^2_{(1)} = 19.085$ $\mathbf{P < 0.001}$	$\chi^2_{(3)} = 188.522$ $\mathbf{P < 0.001}$	$\chi^2_{(1)} = 11.026$ $\mathbf{P < 0.001}$	$\chi^2_{(3)} = 282.426$ $\mathbf{P < 0.001}$

Significant results ($P < 0.05$) are in bold.

patches of the FU plot and significantly lower in the other plots (Table 1; Fig. 6f).

The constrained ordination models, examining the effect of the plot type (location in relation to the road) and of the patch type (shrub vs open), showed significant effects of both plot type and patch type, but not of the interaction between them (plot × patch), on the arthropod assemblage composition (Table 2; Fig. 7).

The RDA plot demonstrated how the fixed factors (the patch type and the location in relation to the road) affected the arthropod assemblage composition (Fig. 7). The first axis (eigenvalue = 0.222) was correlated with patch type, with groups associated with the shrub, such as parasitic Hymenoptera and Aphidoidea, appearing on the right-hand side and groups associated with the open patches, such as Psocoptera and Acari, on the left-hand side. The second axis (eigenvalue = 0.182) divided the plots according to their location in relation to the road, with upstream plots appearing higher and downstream plots appearing lower. This suggests that both patch type and location, in relation to the road, affected the assemblage composition, with the patch type being a more powerful explanatory variable.

Discussion

In this work, we evaluated the effects of a gravel road that runs across a hillslope on ecosystem organization in a hyper-arid region. Based on previous knowledge (e.g., Forman and Alexander 1998, Jones et al. 2000, Brooks and Blair 2005), we assumed that in such a runoff-driven ecosystem, a disturbance will result in the redistribution of the scarce water resources, which, in turn, may cause a state shift in the spatial distribution of shrubs. We predicted that if such a shift indeed occurs, it will have subsequent effects on the abundance and composition of the arthropod assemblage.

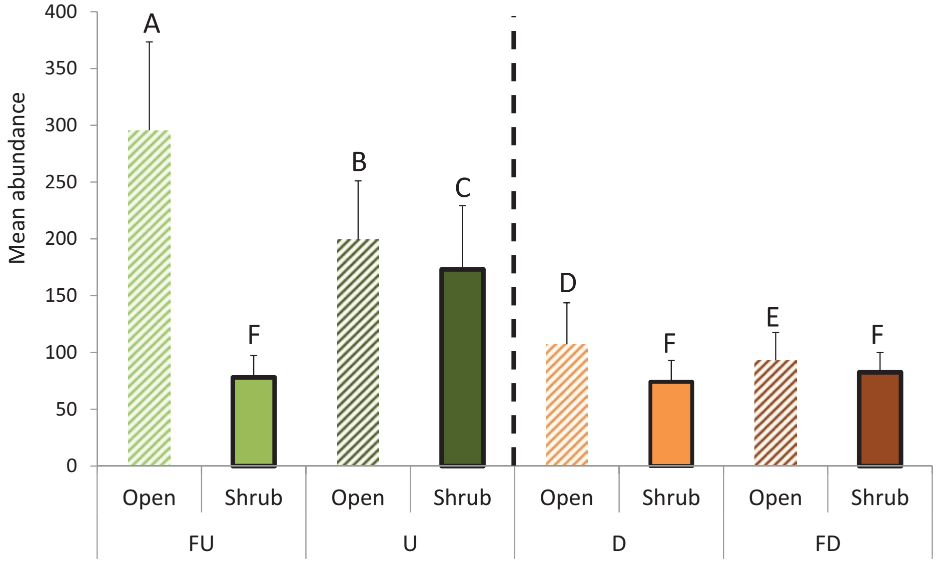

Fig. 5. Mean abundance (±S.E.) of arthropods in open patches and shrub patches in relation to their location with respect to the road in the Ramon study area. U: upstream (immediately above the road), D: downstream (immediately below the road), FU: further upstream (~50 m above the road), and FD: further downstream (~50 m below the road).

Effects of the Road on the Spatial Distribution of Shrub Cover

Consistent with our predictions, we found higher relative cover of shrubs above the road than downstream from it. Indeed, in our study system, the road is slightly elevated above the wadi bed in many places, probably contributing to the accumulation of water in the wadi section that is immediately above the road, where the shrubs tend to cluster, while reducing resource availability in the plots immediately below the road. Moreover, the road's negative effects on shrub cover seemed to persist in the plots that were ~50 m downstream from the road. Similarly, several studies that evaluated the ecological effects of roads have shown that the effects of a road that cuts across a slope on the redistribution of runoff water can lead to the accumulation of resources above the road, at the expense of the runoff water input downstream from it (Forman and Alexander 1998, Forman 2000, Jones et al. 2000, Brooks and Lair 2005), possibly causing water stress to plant communities downstream from the road (Duniway and Herrick 2011, Waddell et al. 2012). Previous studies have also shown that roads that cut across slopes can increase the runoff discharge in some areas, causing soil erosion along the slope (King and Tennyson 1984, Jones et al. 2000, Luce 2002, Donaldson and Bennett 2004). In the arid areas of the Negev Desert, soil erosion is a major threat to the long-term stability and resilience of the ecosystem (Avni et al. 2006), especially where there is a decrease in the relative plant cover (Zuazo et al. 2009).

Effects of the Road on the Arthropod Assemblage

The road further affected the distribution and composition of the plant-associated arthropods. Total arthropod abundance was generally higher in the plots above the road than in the plots below the road. Notably, a significant difference was recorded even between the plot immediately above the road and the plot immediately below the road, which are only separated by ~10 m, with the road as the only likely structure to explain this difference. Previous research has suggested that increased water availability near roads increases vegetation greenness, productivity, and fecundity (Lamont et al. 1994, Klöcker et al. 2006)—effects that may result in an increased herbivore abundance in roadside vegetation (Lightfoot and Whitford 1991, Raiter et al. 2018), as well as in the resultant presence and abundance of higher trophic levels (Fox et al. 1990, Cagnolo et al. 2011, Gordon et al. 2013). Moreover, several studies have noted that when a road cuts across a slope, the effects of the road may be asymmetrical (Forman and Alexander 1998, Forman 2000). Such differences in arthropod abundance are likely to result from the cascading effects of an accumulation of runoff water, higher relative shrub cover and vigor, and possibly, higher accumulation of vegetation litter and organic carbon content, above the road (Lightfoot and Whitford 1991). In accordance, several studies found positive correlations between arthropod abundance and richness and shrub patch area. However, there are differences in the distribution patterns of different functional groups (e.g., ground-active arthropods vs soil-dwelling microarthropods), especially with respect to seasonality (Steinberger and Wallwork 1985, Liu et al. 2012, Meloni et al. 2020).

Interestingly, the differences in arthropod abundance between the plots were more pronounced in the open patches than in the shrub patches, and in the undisturbed open patches, we observed higher arthropod abundance than in any other shrub patch. This may be explained by the generally higher abundance of arthropods in the open patches in dryland ecosystems during the spring, when herbaceous plants are at their peak (Santos et al. 1978, Shelef and Groner 2011, Wasserstorm et al. 2016, Liu and Steinberger 2018). However, while the arthropod abundance in the shrub patches was highest in the plots immediately above the road, following the pattern of the shrub cover, the arthropod abundance in the open patches was the highest in the plots that were ~50 m upstream from the road. This could be due to the high density of herbaceous vegetation in these undisturbed plots (although this aspect has not been quantified), compared to the plots immediately above the road, where the increase in the relative shrub cover might have come at the expense of the herbaceous vegetation, to some extent. Another consequence was that the contrast in arthropod abundance among the patch types (open vs shrub) was higher further upstream (less disturbed habitat) in comparison to the rest of the

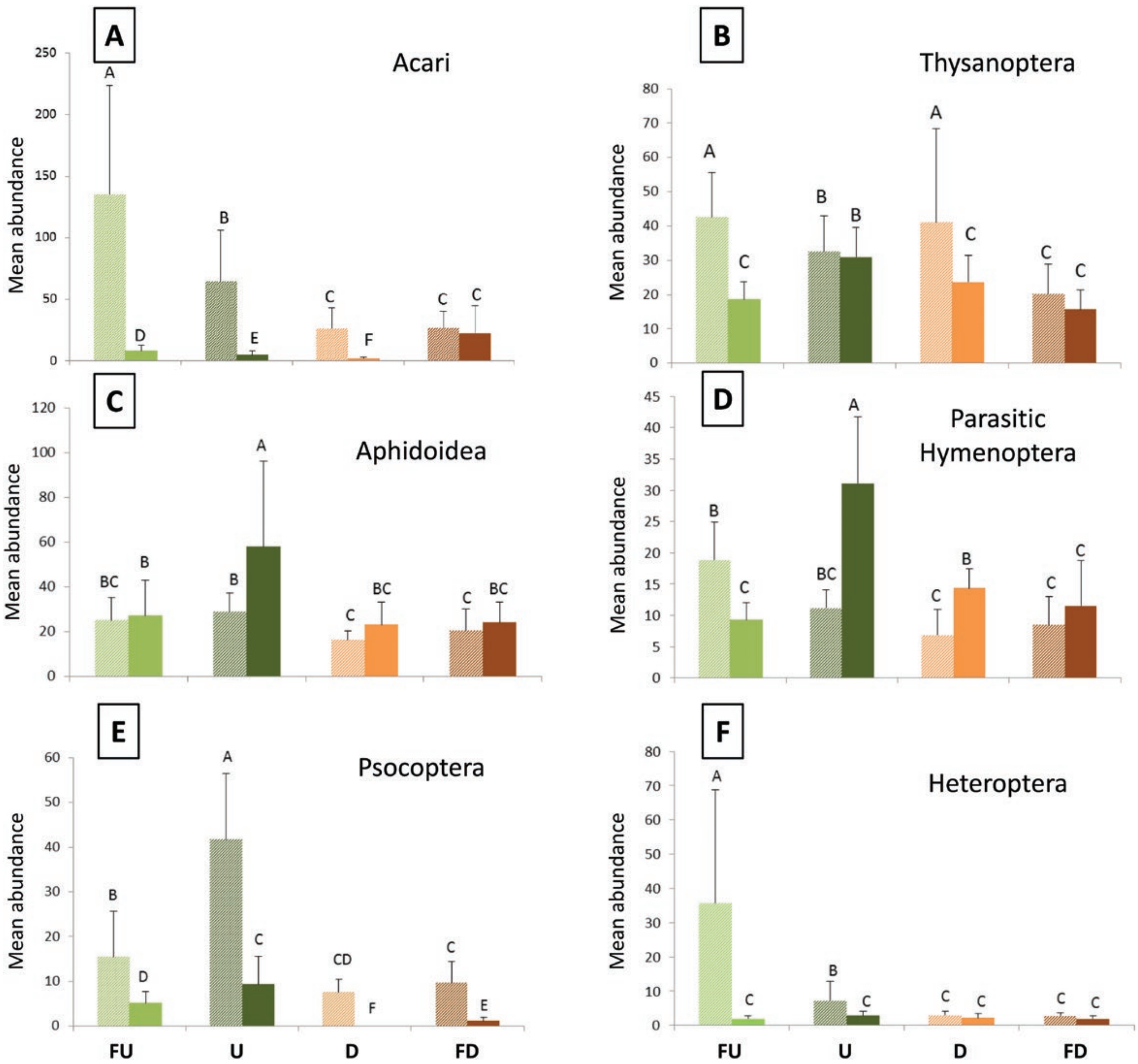

Fig. 6. Mean abundance (±S.E.) of the most abundant taxa in shrub patches and open areas in the different plot types regarding their location with respect to the road in the Ramon study area. Darker shades (right) represent the shrub patches, and lighter shades (left) represent the open patches. FU: further upstream, U: upstream (above the road), D: downstream (below the road), and FD: further downstream.

plots (that were more highly disturbed). Hence, the roads possibly lead to a reduction in patchiness—an aspect representing the complexity and level of organization in the plot (Jørgensen and Nielsen 1998).

Differential Responses of Different Arthropod Groups

We found that most of the common taxonomic groups were significantly affected by both plot type and patch type. The distribution patterns were probably affected by the locomotion capacity of many of the plant-associated arthropods (e.g., walking and phoresis in Acari, direct flight in alate Aphidoidea, parasitic Hymenoptera, and adult Heteroptera and Psocoptera, and perhaps less direct flight in Thysanoptera), enabling them to move into suitable patches according to their nutritional and habitat preferences, possibly combined with higher reproductive rates in these patches (Resh and Carde 2009). The observed pattern might have also been influenced by our sampling method, which aimed at small taxa with relatively high locomotive and reproductive capacity and which are sensitive to environmental fluctuations and disturbances. Sampling methods focusing on other functional groups could have revealed different patterns (Sánchez-Piñero et al. 2011, Liu et al. 2012).

Other patterns may also be revealed in wetter ecosystems, where water flows throughout the year and maintains rich aquatic communities, which may be strongly affected by barrier effects and dispersal limitations posed by the road (e.g., Wemple et al. 2018, Leitão et al. 2018, Brejão et al. 2020). A road cutting through an ephemeral stream in a hyper-arid ecosystem does not seem to create a formidable barrier for highly mobile taxa, such as the plant-associated arthropods that were studied here.

Table 2. Results of multivariate analyses of the constrained (partially constrained RDA) ordinations

Model type	Main effect	Partial variation	Explained variation	Pseudo-*F*	*P*
Constrained	Plot type	656	7.22%	1.6	<0.001
Constrained	Patch type	674	9.77%	6.7	<0.001
Constrained	Patch type* Plot type	13	3.05%	0.6	0.930

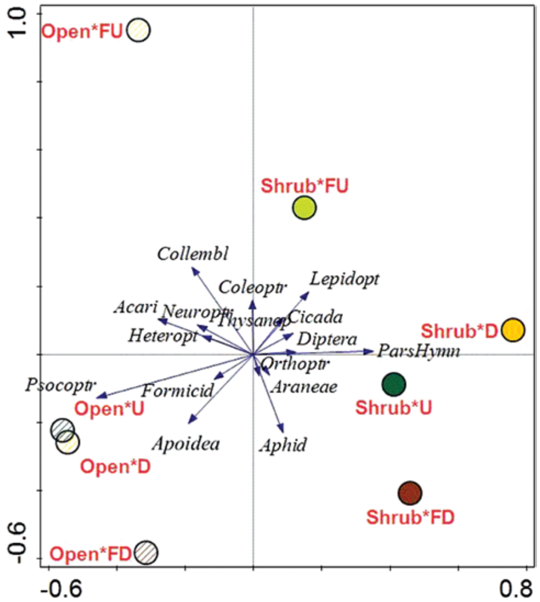

Fig. 7. RDA biplot expressing the relationship between species and the environmental variables. The shortened notations of the taxonomic groups are Aphid (Aphidoidea) Coleoptr (Coleoptera), Collembl (Collembola), Formicid (Formicidae), Heteropt (Heteroptera), Lepidopt (Lepidoptera), Neuroptr (Neuroptera), Orthoptr (Orthoptera), ParsHymn (parasitic Hymenoptera), Psocoptr (Psocoptera), and Thysanop (Thysanoptera). FU: further upstream, U: upstream (just above the road), D: downstream (just below the road), and FD: further downstream.

The responses of some common groups (e.g., Acari and Psocoptera) probably dictated the total arthropod abundance, with higher abundances upstream from the road, as well as in the open patches. It is likely that many Acari and Psocoptera grazed on fungi and algae, which are abundant in the open patches during the spring (Wasserstorm et al. 2016). In particular, Psocoptera are known to increase in numbers in response to soil moisture (Diaz-Montano et al. 2014) and to be more abundant during the early stages of decomposition (Santos et al. 1984). This may explain their high abundance in the plots immediately above the road, which probably accumulated more runoff water and experienced more rapid decomposition processes (Whitford et al. 1988); this pattern is further illustrated by their very low abundance below the road.

Sap-sucking insects (e.g., aphids) were similarly higher in abundance in the shrub patches of the plot immediately above the road where water and vegetation accumulated. The abundance of the parasitoid Hymenoptera was higher in these patches as well, possibly because aphids are important target hosts for many parasitoid wasps (Schmidt et al. 2003, Thies et al. 2005). Nevertheless, in the plots further upstream from the road, parasitoids were more abundant in the open than in the shrub patches. It could be that in these plots, parasitoids were mostly attracted to the flowering herbaceous vegetation as a source of nectar (Jervis et al. 1993). Altogether, it is likely that the composition of the plant-associated arthropod assemblage corresponded with variations in the state, quality, and amount of resources in a patch.

The ordination results also confirmed the importance of the patch and plot type in overall arthropod assemblage composition. The fact that the ordination arranged the data with the patch type as a main driver, correlating to the first (horizontal) axis, suggests that the affinity to the patch type is the more important determinant of the assemblage composition, while the effect of the road disturbance (second, vertical axis) has a significant, but lower magnitude, effect on the plant-associated arthropod assemblage composition. While there was a significant effect of the interaction between patch type and location in relation to the road (plot type) on the total abundance of arthropods, this interaction was not significant in relation to the assemblage compositions. This may be because the assemblages of the shrub patches were not dramatically different among the plots (with the exception of the disappearance of Psocoptera from the shrub patches in D), in comparison with the assemblage composition among the open patches, which showed greater variation (with more Thysanoptera in D, more Psocoptera in U, more Heteroptera in FU, and more Acari above the road).

Our results do not allow us to fully distinguish between the immediate effects of the road on arthropods (e.g., through road kills, pollution, and exposure to predation; Tamayo-Muñoz et al. 2015) and the indirect effects of the road via the redistribution of water resources and the subsequent effects on plants in the ecosystem (Brooks and Lair 2005, Duniway and Herrick 2011, New et al. 2021). Nevertheless, the highly asymmetrical pattern between the upper and lower sides of the road strongly suggests that arthropods are affected by plant state and availability in the various plots and patches (Forman and Alexander 1998, Forman 2000, Brooks and Lair 2005). Such effects may be particularly impactful in ephemeral streams in hyper-arid ecosystems, where the limited input of water is vital and induces high concentrations of organisms in wadis.

Our study illuminates the advantageous use of a relatively simple tool set (i.e., a study of the arthropod assemblage composition and the quantification of shrub cover with remote sensing methods) in the monitoring of an ecosystem's state and the indication of habitat degradation. These are important tools that can be used in locations where the species identification of small insects is not available, making it useful for para-taxonomists and conservation workers. The clear distinction obtained, sometimes even at the order level, demonstrates the differential responses of arthropods to environmental conditions, according to the characteristics, such as the feeding habits and locomotive capacities of various taxonomic groups. Improving the taxonomic resolution may better highlight the effects of the varying environmental conditions on the arthropod assemblage composition.

Finally, our results demonstrate how human-made linear infrastructures can change resource redistribution, subsequently leading to changes in ecosystem structure and function. These effects need to be considered and optimized when implementing such structures in conserved areas, to promote the stability and resilience of arid ecosystems.

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Author Contributions

S.C. is responsible for the data curation, formal analyses, investigation, software, visualization and writing-original draft, editing. M.S. is responsible for the investigation, methodology, project administration, resources, supervision, validation, visualization and writing-reviewing, editing. E.G. is responsible for the conceptualization, funding acquisition, investigation, methodology, supervision and writing- reviewing, editing. A.P. is responsible for the investigation, methodology, data curtion, formal analyses, investigation, resources, software and visualization.

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