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Land-use differences modify predator-prey interactions and Acacia vegetation in a hyperarid ecosystem

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ABSTRACT

Dryland agriculture has extensive impacts on surrounding ecosystems through its unintentional provision of food and water resources to local wildlife. We analyzed the response of a predator community of jackals, wolves and foxes to land-management choices, and how that response in turn affects native gazelles and Acacia vegetation in the Arava Valley of Israel. This hyperarid region is characterized by contrasting regimes comprising privatized (Moshavim) and communal (Kibbutzim) agricultural settlements, which provides ideal conditions for evaluating how land-management differences translate into crop choices, affecting resource availability and ecosystem changes. Integrating multi-year field observations of predators and gazelles with agricultural datasets, we show that shifts in land-use strategies have cascading ecological impacts. This is evident in the association of date orchards, an expanding land use especially in Kibbutzim, with shifts in the geographical and seasonal distributions of predators. Increased predator presence due to resource availability has displaced gazelles farther from settlements, subsequently impacting Acacia seed dispersal and recruitment. Considering the global expansion of dryland agriculture, the evidence of such socio-ecological cascading effects suggests the necessity to approach agricultural management at the landscape scale in desert regions.

1. Introduction

Agriculture is the form of human land modification most significantly associated with biodiversity decline and resource degradation (Maxwell et al., 2016). Increasing global food demand has led to large-scale land conversion to agriculture in drylands (Geist and Lambin, 2004). These arid regions are a large and vital part of human and biophysical environments, supporting nearly 40% of the global human population and diverse land management and agro-ecological systems (Reynolds et al., 2007). Desert ecosystems are especially vulnerable to agricultural overuse (Tal, 2016) and to cascading ecological effects due to invasive species linked with agricultural inputs and water availability (Yom-Tov et al., 2012). Evaluating the impacts of agricultural regime differences and their respective land practices across regions on native desert ecosystems is thus essential to dryland ecosystem management.

Governance processes underlie varied land-use responses to socioeconomic, technological, climatic, cultural and policy factors (Liu et al., 2007), and therefore act as a mediator of land-use patterns. Agro-ecological systems further show stark local and regional differences with regards to governance types, land-management strategies implemented, and their ecological outcomes (Shanas et al., 2006; Jepsen et al., 2015). For example, land tenure can combine with macroeconomic conditions to slow forest loss (Holland et al., 2014), and differences in private versus state-controlled agriculture can affect the extent of natural grazing land in Africa (Homewood et al., 2001). Yet despite accelerated ecosystem changes in drylands at the global scale, changes in ecosystem communities as a result of agricultural regime differences in drylands are rarely investigated.

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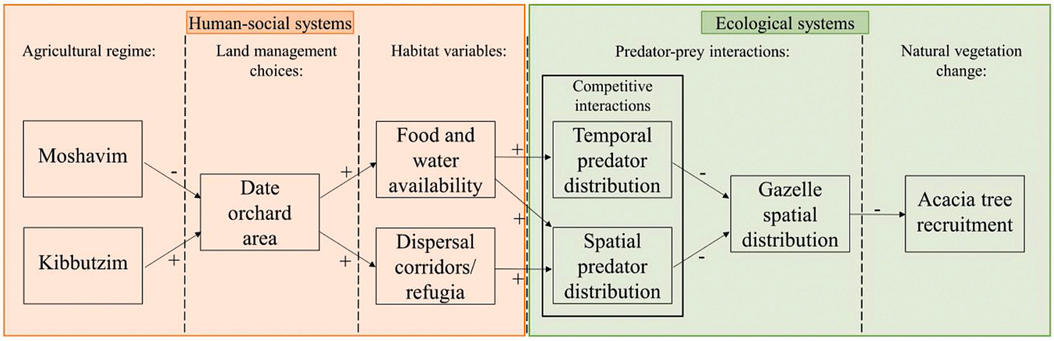

Fig. 1. Expected socio-ecological causal pathways linking agricultural regimes and ecological community changes in the Arava Valley, Israel. Increasing cultivation of date orchards may provide habitat and other resources to predator species, allowing them to expand both their geographic and temporal distributions. Increasing predator distributions may displace native gazelles farther from agricultural settlements. This may reduce new Acacia tree establishment reliant on gazelles for their seed dispersal and germination. Arrows show causal pathway, "+" = positive effect, "-" = negative effect.

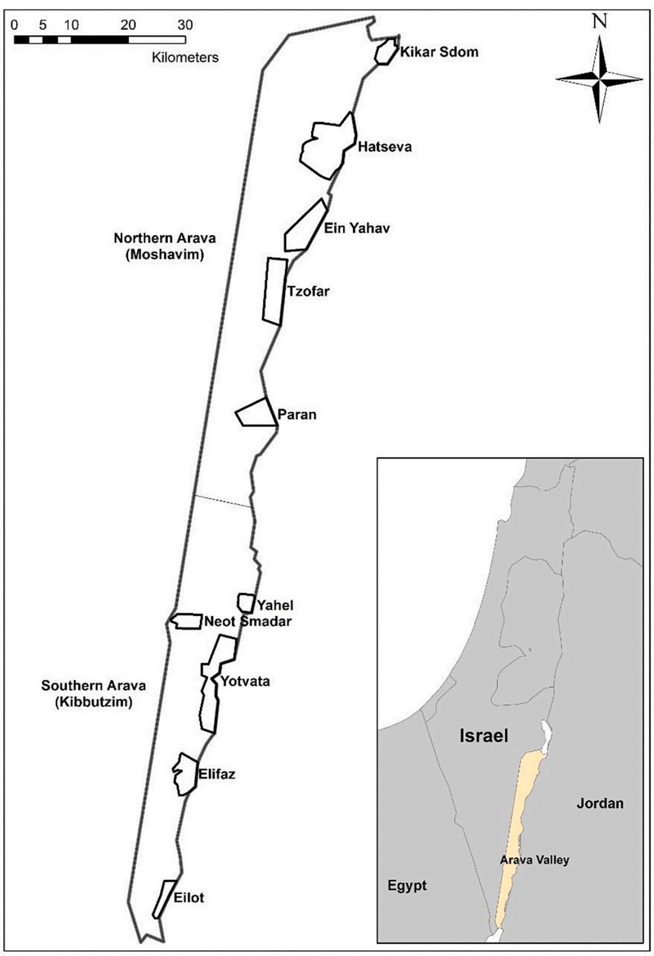

Fig. 2. Map of the Arava Valley showing agricultural settlement blocs. The ~177 km long Arava Valley is located in the southeastern part of Israel (inset). Polygons equal settlement blocs in northern and southern regions (delineated by dashed line) of the Arava Valley, comprising Moshavim and Kibbutzim respectively.

The Arava Valley in Israel is an intensive agricultural region in a hyperarid desert ecosystem, characterized by two unique land-management regimes – privatized cooperative "Moshavim" and socialist collective "Kibbutzim" – with contrasting institutional and cultural approaches to social and economic organization, labour systems, distribution of capital, and decision-making processes, which constrain their respective land- and water-use patterns (Strom, 2016). For example, labour-intensive production of seasonal vegetables in enclosed agricultural structures is the dominant land use of northern Moshavim, comprising farmers with individual land parcels. By contrast, southern Kibbutzim, due in part to an ideology of self-reliance and socialism, are dominated by large, contiguous date palm orchards (herein referrred to as "date orchards") and open, mechanized fields, which are less dependent on external labour (Strom, 2016). Such agricultural land-use disparities in the Arava Valley have been linked to divergent ecological outcomes in terms of, for example, the degradation of natural springs (Bruins et al., 2012), groundwater contamination (Oren et al., 2004), and agricultural pest incidents (Nissim, 2019). Here, we hypothesize that these different regimes and their respective agricultural practices, particularly in relation to date orchard cultivation, have influenced the spatio-temporal distributions of large desert carnivore and ungulate-prey species, with cascading consequences for the germination potential of keystone Acacia vegetation in the region.

The past 10 years have seen the considerable range expansion of invasive and desert predator species due to the increasing availability of food and water resources. These include golden jackals (*Canis aureus*), recent invaders to the Arava Valley especially around southern Kibbutzim, and increasingly abundant Arabian wolves (*Canis lupus*; Barocas et al., 2018) and red foxes (*Vulpes vulpes*; Shapira et al., 2008) – both locally adapted desert species long present throughout the Arava Valley in low numbers especially around southern Kibbutzim. Predator interactions can alter ecological systems through trophic cascades. Top-down mechanisms (e.g. mesopredator release or suppression) affect predator and prey distributions (Ripple et al., 2014), while the outcome of these interactions may rely on bottom-up mechanisms, including resource availability and habitat complexity (Ritchie and Johnson, 2009). In a hyperarid, low-productivity region these limiting bottom-up factors are most likely to regulate predator interactions, and consequently native prey species (Letnic et al., 2011; Newsome et al., 2015). Additionally, seasonal fluctuations due to contrasting land management and crop choices of agricultural regimes influence temporal resource availability, especially in arid agro-ecological systems, affecting species use of different agricultural habitats and their seasonal occurrences (Segre et al., 2019). Recently, expanding date orchard cultivation in both Kibbutzim and Moshavim agricultural landscapes of the Arava Valley has resulted in spatial and seasonal changes in food and water resource availability (Hackett et al., 2013). While whole-ecosystem approaches (e.g. conservation planning) incorporating cascading effects exist (Ritchie and Johnson, 2009), in drylands, management efforts are often limited to landscape-level changes and single species or assemblage shifts tied to human resources, and do not consider cascading ecological effects tied to land-use practices (Rees et al., 2020; Smith and Allen, 2021).

Our research objective is to advance understanding of trophic cascades by investigating the shifting geographical and seasonal distributions of a predator community in response to acute increases in resource availability associated with land-use practices and crop choices in a naturally resource-scarce environment. Our study examines these effects across two contrasting agricultural regimes over the past 10 years in a hyperarid agricultural region of Israel. We focus on the ways that organizational differences between Kibbutzim and Moshavim underlying variation in landscape management and resource availability have affected spatio-temporal predator distributions and their interactions, particularly in association with date orchards, an increasing regional land use. Finally, we examine the impacts of these socio-ecological changes on the distribution of a native gazelle species (*Gazella dorcas*) and their possible role in Acacia recruitment in these intensifying agricultural landscapes. We hypothesize the following: (a) increased resource inputs have attracted invasive generalist species, modifying predator interactions through competition; (b) as a result, the distribution of predator species varies both spatially and temporally due to differences between agricultural settlements in crop choice and resource inputs; and (c) increased overall predator presence has had cascading effects on desert vegetation through displaced prey species, subsequently reducing herbivore-assisted seed dispersal of Acacia vegetation (Fig. 1).

2. Methods

2.1. Study region

The Arava Valley is a narrow area stretching approximately 177 km in southern Israel (Fig. 2). This is a climatically and geographically homogenous hyperarid region receiving an average annual rainfall of 20 mm, with average daily temperatures ranging from 7 °C in winter to 42 °C in summer, and high evapotranspiration rates. Permanent agricultural cropland characterized by Kibbutz (sing. form of Kibbutzim) communal settlements was first initiated in 1957, with a series of agricultural settlements established over the decades. The total population of agricultural settlements in the region numbers nearly 6000 excluding foreign national labourers. Agriculture is still the prominent economic activity, including date orchards, seasonal vegetables, flowers, dairy production, livestock rearing, and aquaculture. Recent years have also seen the growth of renewable energy projects, small businesses and tourism.

Water consumption for agriculture depends almost entirely on brackish groundwater sources (with decreasing water-tables), limiting crop yields and inhibiting salt-sensitive crop types (Tripler et al., 2011). However, agriculture remains highly productive in terms of yield per area due to modern agricultural technologies such as drip-irrigation systems, in addition to a relatively mild winter providing out-of-season price incentives for winter crops suited to European markets (Bruins et al., 2012). As mentioned in the introduction, the Arava Valley is divided into two distinct governance areas with clear differences in their agricultural crop regimes and consequently land configurations (Figures A.1 and A.2). The socialist Kibbutzim in the south, where land, costs and profits are shared among members and decisions are made collectively (Sagie et al., 2013), are characterized by large contiguous plots of open fields and date orchards. Date orchards were historically cultivated in Kibbutzim because these are better able to bear relatively high initial capital costs and make long-term investments (Baland and Francois, 2005). The northern Moshavim, where land is managed individually (Kislev, 2015), are larger in terms of total agricultural area and population size, more intensive in terms of water consumption and other inputs (Strom, 2016), specializing in seasonal vegetable farming (especially pepper) under agricultural structures such as net-houses and tunnels, and highly reliant on foreign labour. These differences cause changes in resource abundance and seasonal availability, allowing us to evaluate the role of land-use practices, specifically crop regimes, in modifying predator spatio-temporal distributions and consequently, native prey distributions.

2.2. Predator spatial distributions, range overlaps and invasion frontiers

We obtained data from the Israel Nature and Parks Authority (INPA) on the occurrence records of 2074 golden jackals, 1491 Arabian wolves and 2632 red foxes in the Arava from 2011 to 2018 – a period coinciding with shifting agricultural crop regimes (i.e. from pepper to date cultivation), and the increased abundance of predators beginning in the southern Arava including their dispersal into the northern Arava. Other local predators during the time period occurred less frequently and are therefore not considered – *Hyaena hyaena* (n = 588), *Vulpes rueppellii* (n = 10). Stray dogs (*Canis familiaris*) are very recent invaders to the region (from Jordan), and increasingly abundant since 2018 (n = ~300; Nissim, 2019), and therefore also not considered here. Occurrence data include direct observations of species and track records (~10% of occurrences) by several knowledgeable INPA park rangers. Rangers survey all Arava Valley regions consistently throughout the year, recording their observations (using GPS to mark coordinates) on our species of interest and all vertebrates in the region, thus controlling for observer bias. Additionally, all data are reported to INPA officials, where data are integrated, synthesized and assessed for quality control (e.g. double-counting, valid coordinates, etc.).

Occurrence records of predator species based on GPS coordinates were converted into point localities and used to create kernel density estimations (KDE using ArcGIS 10.3) by calculating the number of times a species occurs within a 10 m environment using a kernel function to fit a smooth surface to each point. The kernel smoother is an effective approach to standardizing species density occurrences in a geographical space, independent of sampling effort and resolution (Broennimann et al., 2012) in order to model the space probability and landscape changes over time of each species and their measured overlap. This is an especially effective approach when dealing with large sample sizes and low dimensional systems (Qiao et al., 2017) such as ours. To assess the range overlap of predator species, we used the *D* metric (Warren et al., 2008) on KDEs to measure the yearly pairwise overall match between predator distributions, ranging from 0 (no overlap) to 1 (complete overlap).

D metric to measure yearly pairwise overall match between species distributions is calculated as:

$$D = 1 - \frac{1}{2}\sum_{ij}\left(\left|Z_{1ij} - Z_{2ij}\right|\right)$$

Where Z_{1ij} is species 1 occupancy and Z_{2ij} is species 2 occupancy. We used the *nicheOverlap* function of the *dismo* package using R version 3.4.3 (R Development Core Team, 2017). Predators are clearly delineated by trophic structure (Arbel, 2008) with wolves as the apex predator (~20 kg in body size, and up to 17 individuals per pack), followed by invasive and mesopredator jackals (~8.5 kg in body size, and usually in breeding pairs or small packs when resources are high), and foxes (~3.2 kg in body size, often solitary). Therefore, we expect that wolves will overlap with the other predators to a lesser degree due to top-down suppression.

We also measured the north- or southward shift of predator species' ranges based on yearly latitudinal occurrence in order to capture their median range changes and invasion frontiers. To determine range expansion or contraction of species distributions, we measured their northern and southern range margins by the 90th and 10th quantile lines of yearly latitudinal occurrence. Thus, we define an invasion frontier as the latitudinal point south of which 90% of species occurrences are located.

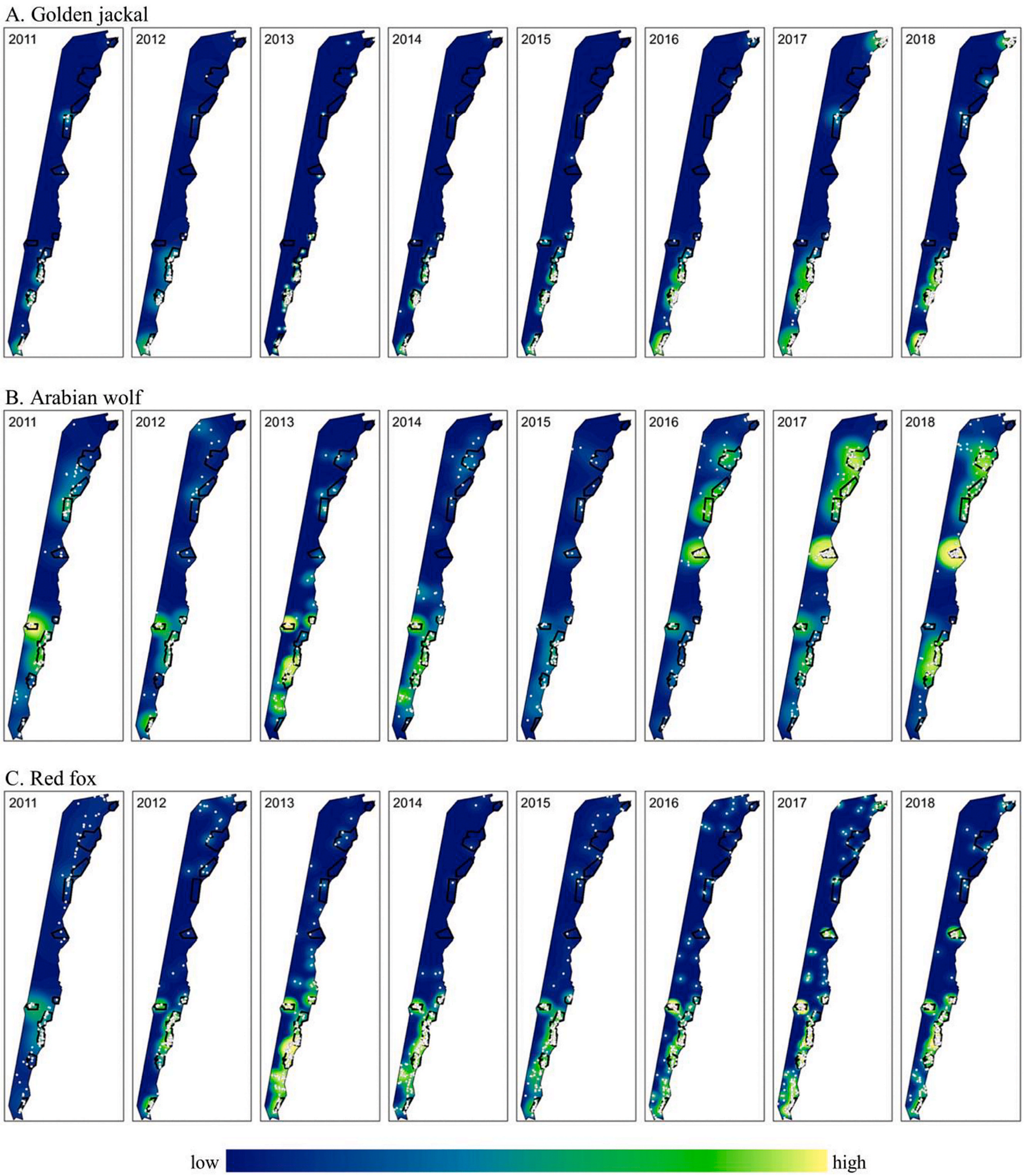

Fig. 3. Changes in the spatial distribution of occurrence records of (A) golden jackals (*Canis aureus*), (B) Arabian wolves (*Canis lupus*), and (C) red foxes (*Vulpes vulpes*) in the Arava Valley between years 2011–2018. Distribution patterns were summarized with kernel density estimates to show probabilistic distributions within a 10 m radius represented by colour codes from low (blue) to high (yellow). White circles correspond to species occurrences. Black polygons correspond to settlement bloc borders. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.3. Land- and water-use trends

In order to analyze the role of agricultural land-use classes and resource differences between Kibbutzim and Moshavim explaining predator distributions, we related predator abundance within settlements to five of the predominant agricultural land- and water-use variables: (1) date orchard area (Dunams = 0.1 ha; data from Israel Date Growers' Cooperative) – data was provided in terms of number of individual trees per settlement, which we divided by 12.5 to approximate the number of trees per Dunam (the standard spacing of growing date orchards throughout the region; Figure A.3) and hence total date orchard area, (2) vegetable area (Dunams, all seasonal crops; data from Agricultural Committee of the Central Arava Regional Council, and Southern Arava R&D), (3) livestock enclosure area (Dunams, all non-

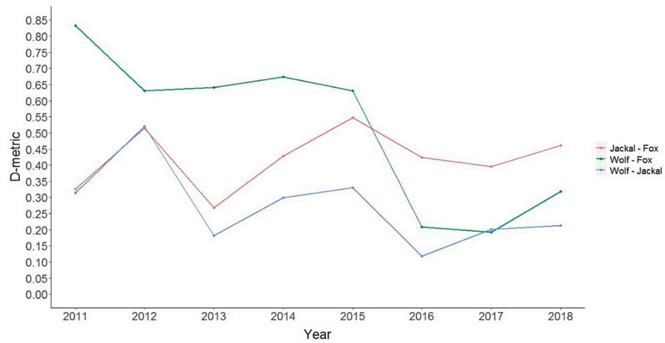

Fig. 4. Distributional overlap using *D* metrics measuring overlap between golden jackals (*Canis aureus*), Arabian wolves (*Canis lupus*), and red foxes (*Vulpes vulpes*) between years 2011–2018. *D* metrics were calculated pairwise (e.g. jackal vs. fox) based on kernel density estimates of the occurrence records for each species (from Fig. 3). *D* metric ranges from no overlap (0.0) to complete overlap (1.0). Colours represent combinations between species (blue = wolf and jackal, green = wolf and fox, red = jackal and fox). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

roaming goats, cattle and sheep housed in cattle enclosures; data from Agricultural Committee of the Central Arava Regional Council, and Southern Arava R&D), (4) solar panel area (Dunams, Southern Arava R&D), and (5) agricultural water consumption per area (m^3/Dunam total agricultural area; data from WaterArava of the Central Arava Regional Council, Southern Arava R&D, and Mekorot), representing agricultural water-use intensity and therefore availability to wildlife.

2.4. Hierarchical partitioning and Generalized Linear Models

We used hierarchical partitioning to assess the average contribution of land- and water-use predictors (Murray and Conner, 2009) to the variance in monthly abundance records for each predator species for 2011–2018 within settlement blocs. "Settlement bloc" refers to adjacent settlements (less than ~1 km apart) that we merged into blocs by drawing polygons (using ArcGIS v10.3). Thus, the region was divided into five settlement blocs of Kibbutzim and Moshavim each in the southern and northern Arava respectively (Fig. 2) – the spatial unit of all statistical analyses that we used to intersect with the monthly abundance records of predator species (our response variable). We further calculated coefficient estimates for each model by fitting Generalized Linear Models (GLMs) with *Poisson* distributions, analyzing model goodness of fit by comparing null and residual deviances (with reduced residual deviances supporting improved model fits; Table A.1). We tested variables for collinearity using variance inflation factors (VIF) and found none (VIF scores < 2.5, Craney and Surles, 2002). We constructed GLM and hierarchical partitioning models for each species, and separated each model by agricultural regime (i.e. Kibbutzim and Moshavim) using:

$$\text{Abundance}_{t(regime)} = \text{Date}_t + \text{Vegetable}_t + \text{Livestock}_t + \text{Solar}_t + \text{Water}_t \tag{1}$$

where 't' is monthly time period (between 2011 and 2018), 'Date' refers to date orchard area, 'Vegetable' is vegetable area, 'Livestock' is livestock enclosure area, 'Solar' is solar panel area, and 'Water' is water consumption per total area. Models were constructed using *glm* and *hier.part* functions and package (v1.0-4) using R v3.4.3.

2.5. Seasonal changes in predator distributions

To compare variation in predator monthly abundances, we used Generalized Additive Models (GAMs) with *Poisson* distributions to test for non-linear seasonal trends in jackal, wolf and fox monthly abundances. Seasonal trends were incorporated using month of occurrence as a predictor fitted by cyclic cube regression splines, in addition to the agricultural land- and water-use covariates mentioned above, and maximum temperature of warmest month between years 2011–2018 (data from the Israel Meteorological Society; ims.data.gov.il) to capture environmental factors that may influence predators' seasonal behaviour. For settlement blocs with missing temperature data we used the data of the nearest adjacent settlement. The monthly abundance GAM for each species (separated by agricultural regime) had the following structure:

$$\begin{aligned}\text{Abundance}_{t(regime)} = {} & \text{Year}_t + \text{s}(\text{Month},\ \text{bs} = \text{"}cc\text{"})_t + \text{s}(\text{Date})_t \\ & + \text{s}(\text{Vegetable})_t + s(\text{Livestock})_t + \text{s}(\text{Solar})_t \\ & + \text{s}(\text{Water})_t + \text{s}(\text{Temp.})_t \end{aligned} \tag{2}$$

where 's' represents a smoothing spline function applied to all continuous predictor variables (except livestock and solar panel area), and 'Temp.' is maximum temperature of warmest month (see eq. (1) for remaining variables). Models were constructed using the *gam* function of the *mgcv* package using R v3.4.3.

2.6. Predator effects on gazelle distributions

We hypothesized that the increasing presence of predators has displaced gazelles farther from agricultural settlements due to predator avoidance (Shalmon et al., 2019). We therefore measured the Cartesian minimum distance of predator species occurrences to the nearest settlement bloc centroid buffered by 250 m (using ArcGIS v10.3), by year from 2011 to 2018 and separated by agricultural regime (i.e. Kibbutzim and Moshavim). Gazelle (*Gazella dorcas*) distance was similarly measured in order to capture the effect of predator presence on gazelle proximity to settlements (data on 5760 gazelle occurrence records; NPA). Other large ungulates occurred less frequently and are therefore not considered – e.g. *Capra nubiana* (n = 641), *Gazella arabica* (n = 30 as of 2019; Shalmon et al., 2019), and recently reintroduced *Oryx leucoryx* and *Equus hemionus*. To evaluate significant differences in distance to settlement among predator species and gazelles by agricultural regime, we performed a one-way ANOVA test and Tukey multiple pairwise comparison of means. Statistical analyses were performed using R v3.4.3 and the functions *gdistance*, *aov*, *TukeyHSD* and the package *gDistance*.

2.7. Gazelle effects on Acacia seed dispersal and recruitment

We further hypothesized that as a result of gazelle displacement, Acacia seedlings will be found farthest from settlements because of the function of these herbivores in the dispersal and germination of Acacia seeds, and therefore the establishment of young trees (Ward and Rohner, 1997). To test whether gazelles play a role in Acacia tree recruitment, we measured (a) the distance of Acacia seedlings to settlements, and (b) the direct overlap of these trees with shifting gazelle distributions. We obtained data from the Open Landscape Institute (OLI; deshe.org.il) on the distribution records of 1963 Acacia trees from a 2013 survey (comprising three species – *Vachellia pachyceras*, *V. raddiana* and *V. tortilis*), categorized by tree canopy size (0–2 m, 212 records; 2–5 m, 560 records; 5–10 m, 740 records; >10 m, 451 records). Acacia trees were sampled over 142 different survey sites of 10 Dunams in area each (10 Dunams = 1 ha) throughout the Arava Valley (Figure A.4), thus controlling for a wide range of environmental variables that may influence Acacia vegetation and recruitment (e.g. soil substrates, dry river channel widths, distance to roads, agricultural settlements; OLI, 2013). The smallest tree size category (0–2 m) is used as a proxy for seedlings in order to test whether gazelle distributions are correlated with these trees that may be reliant on them for their recruitment (Stavi et al., 2015). We measured the distance of Acacia trees to agricultural settlements as above for predators and gazelles, performing a one-way ANOVA test and

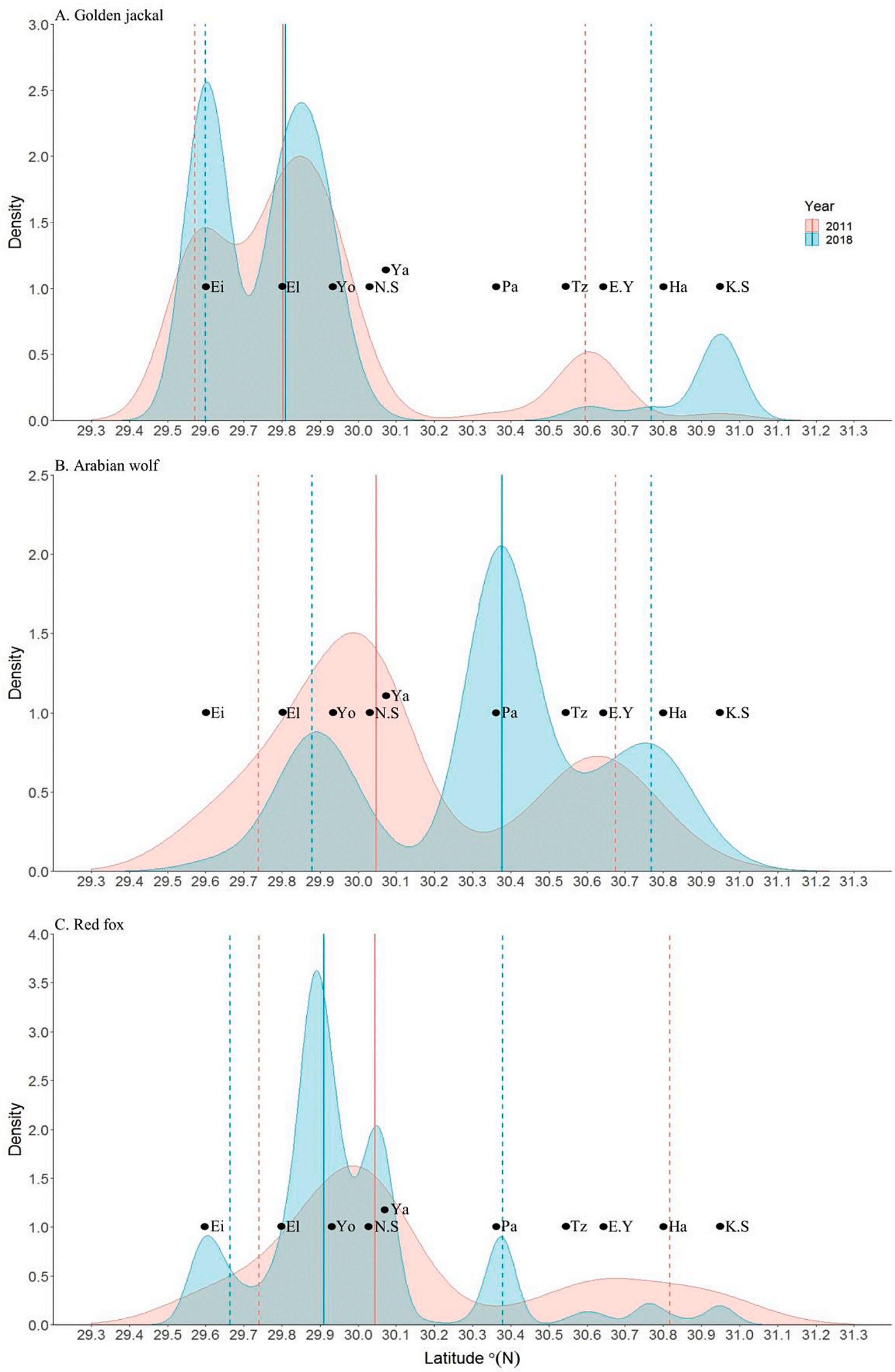

Fig. 5. Latitudinal range shifts in median latitudinal occurrence of (A) golden jackals (*Canis aureus*), (B) Arabian wolves (*Canis lupus*), and (C) red foxes (*Vulpes vulpes*) between years 2011 (red) to 2018 (blue). Shaded areas represent kernel density estimates of smooth distributions of latitudinal occurrence records. Solid lines = median, dashed lines = 10th and 90th percent quantiles. Ei = Eilot, El = Elifaz, Yo = Yotvata, N.S = Neot Smadar, Ya = Yahel, Pa = Paran, Tz = Tzofar, E.Y = Ein Yahav, Ha = Hatseva, K.S = Kikar Sdom – agricultural settlement blocs. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Tukey multiple pairwise comparison of means among tree size categories. We predicted that if gazelles are responsible for Acacia recruitment, then seedlings will be found farthest from settlements, correlated with gazelle distances to settlements.

Acacia take between roughly several to 20 years to reach a canopy size of up to 2 m (contingent on environmental and biophysical factors, example flood waters, slope, soil type; OLI, 2013; Benny Shalmon pers. comm.). Therefore, if gazelles do indeed play a role in Acacia recruitment and their distribution has shifted over time, then we predicted that gazelle distributions in years prior to 2013 will be more congruent with the distribution of Acacia seedlings (0–2 m canopy size) in 2013 than gazelle distributions in the years subsequent to 2013. To test this hypothesis we measured the direct overlap of gazelles with Acacia seedlings. We created Kernel Density Estimates (KDEs) from point locality records (as described for predators in section 2.2) for Acacia seedlings (from year 2013) and gazelles from respective years between 2010 and 2014 (data on 2923 *Gazella dorcas* occurrence records; NPA). KDE layers were converted into 95 percent polygons using the R function *raster.vol*, in order to intersect yearly gazelle distributions with Acacia seedlings of 2013. From respective yearly intersected Acacia and gazelle layers between 2010 and 2014, we extracted density values controlling for spatial autocorrelation by sampling a random 10% of points using the Create Random Points Tool with balanced sampling in ArcGIS. We used Pearson's Correlation to find the relationships of densities between respective yearly Acacia seedlings and gazelle overlaps.

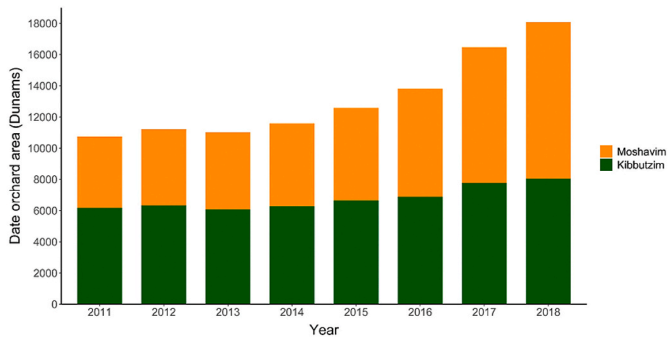

Fig. 6. Yearly trends of total date orchard area by agricultural regime: A) Moshavim (gold bars), and B) Kibbutzim (green bars). (1 Dunam = 1000 m^2 = 0.1 ha). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3. Results

3.1. Predator spatial distributions, range overlaps and invasion frontiers

KDE probabilities (Fig. 3) show that the density of jackals has increased near southern Kibbutzim over time (except in two small settlements), and in the most northerly Moshav settlements. Jackals are absent from the large open desert area delineating southern Kibbutz and northern Moshav regions (~70 km). Wolves consistently remain abundant around most southern Kibbutzim, but since 2015 have increased in most northern Moshavim. Foxes remain abundant in southern Kibbutzim and are widely dispersed throughout the north. Range overlaps between species were estimated by two-way comparisons using *D* metrics (Fig. 4). Spatial overlap of wolves declined both with foxes (D = 0.83 in 2011 and 0.32 in 2018), and with jackals (D = 0.31 compared to 0.21), while that of jackals and foxes increased over the years (D = 0.33 compared to 0.46).

Latitudinal range shifts between years 2011 and 2018 (Fig. 5) indicated that while the median occurrence of jackals remains centered around 29.8°N, their density has increased and importantly, their invasion frontier, as indicated by the 90th percentile line, has expanded further north (30.8°N in 2018 vs. 30.6°N in 2011). Wolves have significantly shifted their median distribution northwards from 30.05°N to 30.4°N (~50 km), while their northern edge remains similar (30.7°N to 30.8°N). The median location of the distribution of foxes has shifted south slightly (30.05°N to 29.9°N), while their northern invasion frontier extent has contracted substantially south (from 30.8°N to 30.4°N).

3.2. Land- and water-use trends and their associations with predator species

Since 2011 date production has become the predominant form of agricultural land use in Kibbutzim, and it has become increasingly significant in Moshavim, especially since 2015 following the collapse in the pepper export market (Fig. 6). Since 2015 date area has increased by 119% in northern Moshavim surpassing total date area of Kibbutzim, which has increased by 31% over the same time period. Solar panel fields for renewable energy are found only in Kibbutzim. Livestock enclosure area is relatively low compared to other land classes in both Kibbutzim and Moshavim and consistent in terms of area over time. These agricultural crop regimes underlie both the amount and timing of water consumption (Fig. 7) based on the water needs of specific crop regimes, their harvest and cultivation periods and corresponding environmental temperatures. Moshavim, specializing in seasonal pepper and other vegetables, traditionally show monthly water consumption profiles with bimodal peaks – the first and largest peak around October during vegetable cultivation when temperatures are still relatively hot, followed by a second peak around April during the vegetable harvest. During summer months no vegetable crops are grown in order to conserve water and to allow for a period of solar sanitization against fungal diseases and pests. Kibbutzim specializing in date production display monthly agricultural water consumption profiles with peaks during the hottest summer months (June, July, August), when perennially grown dates consume the most amount of water. Increasing trends in date production are reflected in an emerging peak in agricultural water consumption to the hottest summer months, which complemented by the bimodal water consumption peaks associated with seasonal vegetables, results in a flattening of the water consumption curve in recent years.

The results from the *Poisson* GLM (Fig. 8) show that jackals are positively correlated with date orchard area in both Kibbutzim ($\beta = 1.73^{-3}$) and Moshavim ($\beta = 1.46^{-3}$), while hierarchical partitioning results indicate that date orchard area explains much of the variation in jackal abundance among Kibbutzim (62%) and Moshavim (43%). Jackals are also negatively correlated to vegetable area in Moshavim ($ß = -9.05^{-4}$), which explains 42% of the variance in abundance here. Date orchard area also explains most of the variance in wolf abundance in Kibbutzim (25%) and are positively correlated with wolf abundance in Moshavim ($\beta = 3.05^{-3}$), but explain less variance there (17%) than other significantly correlated variables such as livestock (48%) and water-use (21%). Foxes are positively correlated with date orchard area ($\beta = 2.89^{-4}$) and livestock ($\beta = 1.90^{-2}$) around Kibbutzim, explaining 31% and 40% of their abundance variation respectively. Around Moshavim, foxes are positively correlated with water-use ($\beta = 9.54^{-3}$) and livestock ($\beta = 1.53^{-2}$), explaining 34% and 20% of their abundance variation, and negatively correlated with vegetables ($ß = -2.25^{-4}$), explaining 39% of their abundance variation. All species are negatively tied to solar panel fields in Kibbutzim.

3.3. Seasonal changes in predator distributions

Generalized Additive Models (GAMs) were constructed based on monthly abundance records for each of jackals, wolves, and foxes from 2011 to 2018 (Fig. 9). Predators display patterns of peak seasonal abundance around hot mid-summer months around Kibbutzim (Fig. 9D–F). Around Moshavim, the seasonal abundances of wolves and foxes are spread more evenly across the middle of the year, and more variation is evident between their respective models' residuals (i.e. standard error) around these settlements (Fig. 9B and C). Around Moshavim over the same period, jackals have yet to invade in significant numbers, making seasonal trends here difficult to interpret (Fig. 9A).

3.4. Predator effects on gazelle distributions and Acacia seed recruitment

Predators occur increasingly closer in proximity to all settlements especially since expanding their distributions (Figures A.5 & A.6). Native desert gazelles occur farther from southern Kibbutzim over the years as predators increase in abundance and proximity, but significantly closer to Moshavim as of 2018 (albeit still relatively distant to these settlements) as predators have yet to establish around Moshavim.

3.5. Gazelle effects on Acacia seed dispersal and recruitment

We predicted that if gazelles play a role in Acacia recruitment, then their distributions should correlate with the distribution of Acacia seedlings. Our results show that the smallest tree canopy size category of Acacias (0–2 m – a proxy for seedlings) from 2013 occur significantly farther to all settlements than larger (and more mature) trees (Fig. 10). These Acacias from 2013 are additionally more congruent with gazelle distributions in 2010 and decrease linearly in overlap from 2010 to 2014 ($r = 0.43$ to -0.31; Figure A.7), supporting our hypothesis that Acacia seedlings from 2013 are more congruent with gazelle distributions prior to 2013.

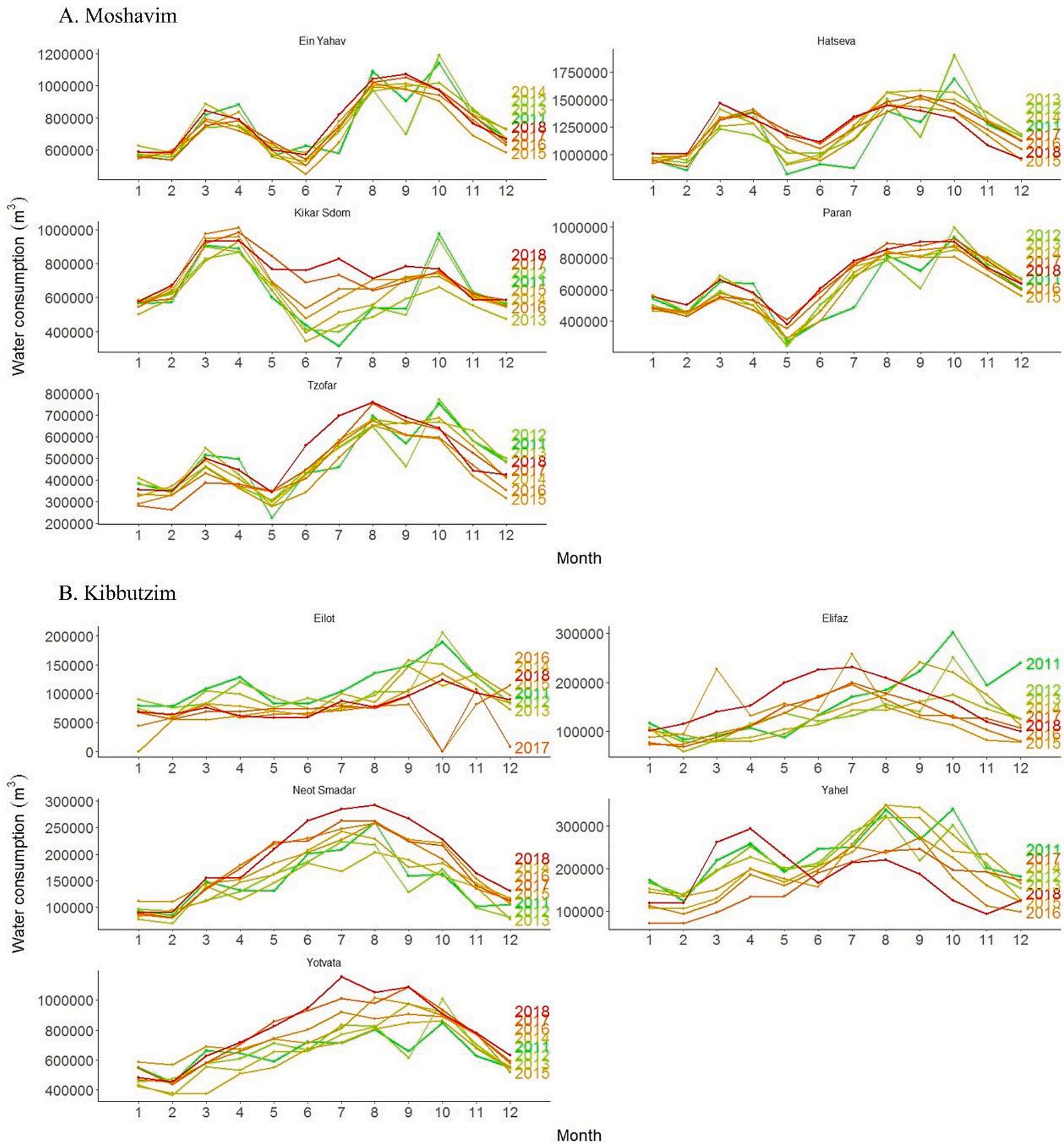

Fig. 7. Monthly agricultural water consumption profiles for settlement blocs: A) Moshavim and B) Kibbutzim. Colours represent different years, from cold (green) in 2011 to warm (red) in 2018. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

Land management differences and crop choices associated with resource influxes may have particularly extensive ecological impacts on fragile and resource-limited dryland ecosystems (Malagnoux et al., 2007). Considering the global expansion of dryland agriculture, and complex socio-ecological and land management systems (Geist and Lambin, 2004), it is important to evaluate the regional impacts of agricultural regimes and their subsequent land-use practices on ecological communities. We investigated the distributional shifts of a predator community and its impact on native ecosystems as a response to crop choices of two distinct agricultural regimes with different water and resource inputs in the hyperarid Arava Valley. We show that predators have expanded their geographic and seasonal distributions with altered competitive interactions in response to increasingly available resources in agricultural settlements linked to expanding date orchards. These changes have cascading effects on native gazelle distributions, which in-turn may impact Acacia tree coverage in the region through reduced herbivore-assisted recruitment.

Land-use practices and crop choice differences between Moshavim and Kibbutzim with distinctive patterns of resource influxes influence the distribution of predator species in the region, most notably through the effect of the expansion of date orchards on jackal distributions (Fig. 8). Historically, Kibbutzim, because of their collective management, were better able to bear the high initial capital costs associated with date orchard cultivation, leading to greater expansion of date orchards in these settlements (Strom, 2016). Thus, it appears that jackals first invaded southern Kibbutzim due to bottom-up resource factors associated with a preponderance of date orchards supporting these non-desert-adapted animals' strong dependence on refugia, perennial

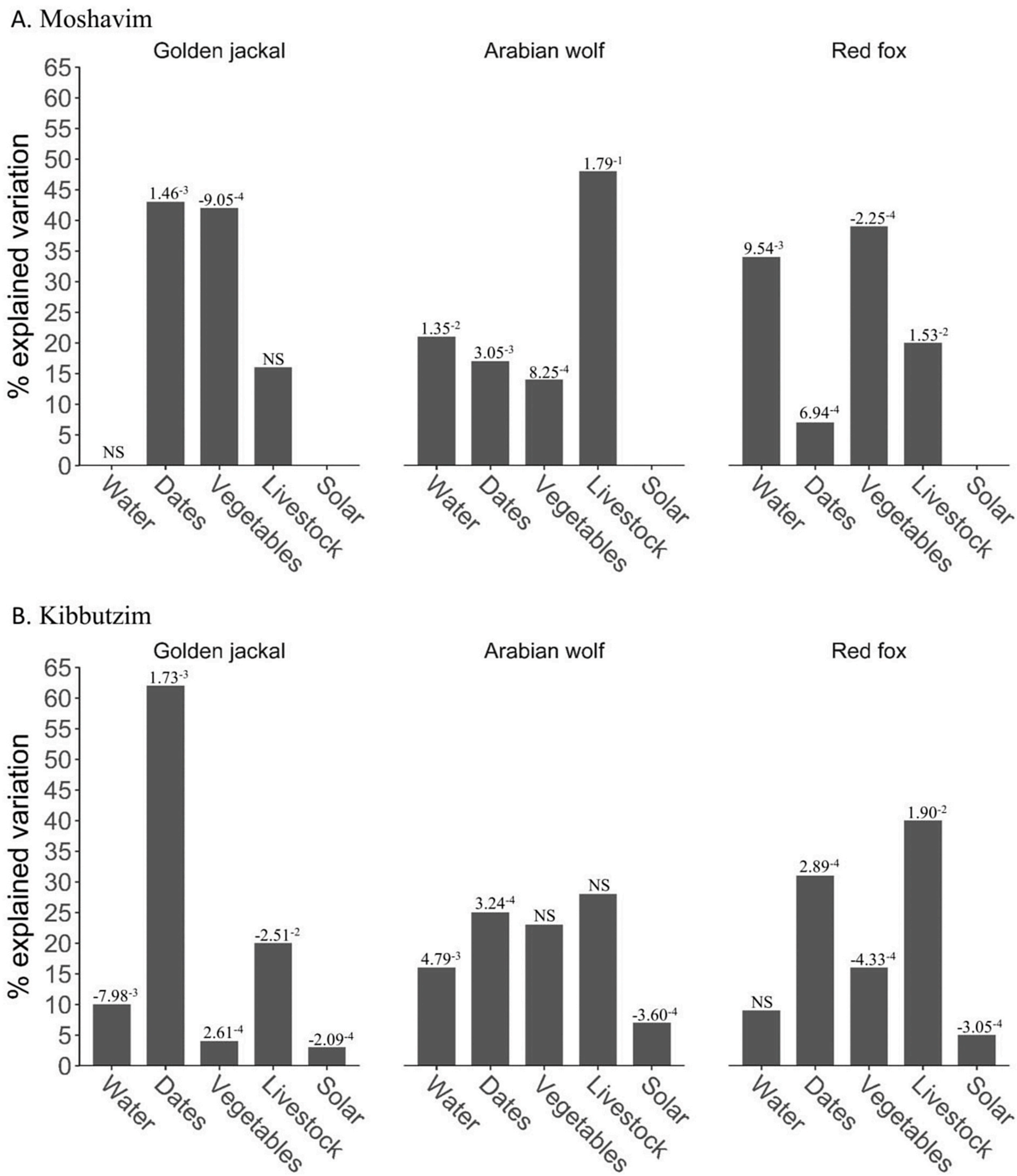

Fig. 8. Relative importance and correlates of land- and water-use predictors of golden jackal (*Canis aureus*), Arabian wolf (*Canis lupus*) and red fox (*Vulpes vulpes*) abundances using hierarchical partitioning and *Poisson* Generalized Linear Model (GLM) regression coefficients from 2011 to 2018 aggregated by agricultural regime: (A) Moshavim and (B) Kibbutzim. Numbers above bins are GLM regression coefficients. All predictors are significant where indicated ($p < 0.05$), and not significant where indicated by NS. Degrees of freedom (d.f.) = 450 per species in Moshavim, 439 per species in Kibbutzim.

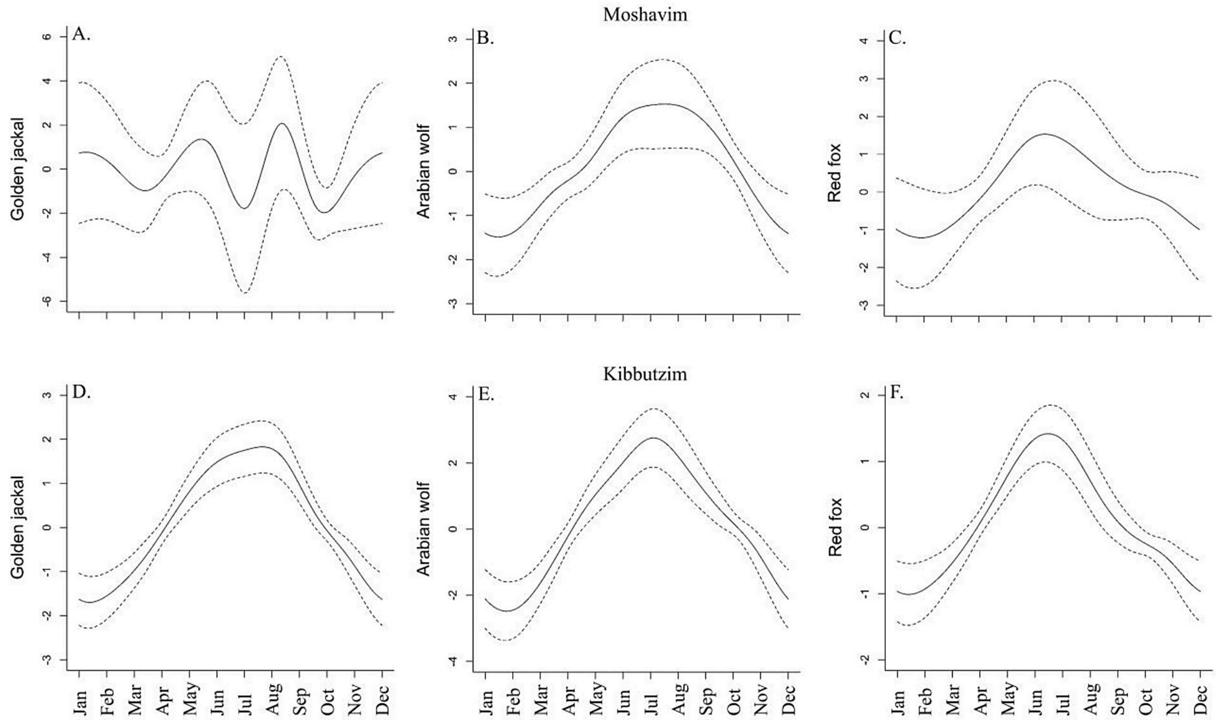

Fig. 9. Monthly abundance patterns of golden jackals (*Canis aureus*), Arabian wolves (*Canis lupus*) and red foxes (*Vulpes vulpes*) from 2011 to 2018 aggregated by agricultural regime: (A–C) Moshavim, and (D–F) Kibbutzim, using Generalized Additive Models. $p < 0.001$ for all figures. Dashed lines represent model standard error.

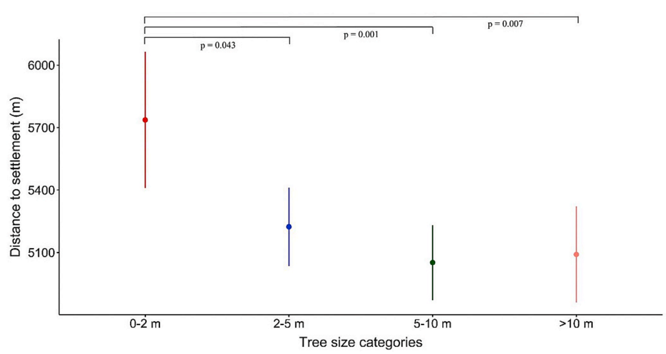

Fig. 10. Differences in Acacia tree spatial proximity to agricultural settlements in 2013. Lineplots = 95% confidence intervals. Tree size canopy categories are: red = 0–2 m (representing seedlings), blue = 2–5 m, green = 5–10 m, orange = >10 m. P-values denote significance using Tukey multiple comparisons of means between tree size categories. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

resources and water readily available from exposed drip-irrigation infrastructure and prolonged daily irrigation hours (similar to findings on the effect of resource subsidies on predators globally; Newsome et al., 2015). In contrast, privatized Moshav cooperatives – specializing in seasonal vegetable cultivation (due to market incentives and foreign labour availability) with different resource inputs and temporal patterns, under enclosed agricultural structures – were less suited to invasive jackal establishment. This demonstrates how agricultural land-use choices and subsequent resource differences constrained by organizational and cultural systems may impact native desert ecosystems. Effects of agricultural landscape differences between Moshavim and Kibbutzim are less marked for wolves and foxes, which have long been present in the Arava Valley (albeit in low abundance until recent years; Mendelssohn and Yom-Tov, 1999) and are thus associated with several agricultural and environmental resources (Fig. 8). Scat analyses in the region reveal that wolf diets contain cow carrion, fruit and garbage (Hefner and Geffen, 1999), supporting our finding that wolves exploit a wide range of agricultural subsidies around both Kibbutzim and Moshavim.

The predators investigated show clear differences in their northern invasion frontiers over the past decade, coinciding with the expansion of date orchards and agricultural resources underlying their distributions. Historically, only foxes were abundant around northern Moshavim, but wolves, which have extensive dispersal distances (50–200 km; Hefner and Geffen, 1999), have significantly expanded from their southern range since 2011 (Fig. 5). Only in recent years have jackals, which are dependent on agricultural settlements for their food and water requirements, invaded the northernmost Arava settlements (with increasing date orchard extents); however not from the southern Arava like wolves, but rather from the northern Jordan Valley thereby expanding their northern invasion frontier. Differences in the expansion of date orchards between Kibbutzim and Moshavim, in conjunction with dispersal and trophic level differences among predators, have led to contrasting outcomes in their interactions (Figs. 3 and 4). As a result, patterns of spatial segregation appear over time, especially in relation with wolves, the apex predator in the region, around southern Kibbutzim (Fig. 3). Jackals occur most frequently in settlements where wolves are least abundant, suggesting a possible mechanism of top-down control whereby in small settlements wolves suppress jackals (Ritchie and Johnson, 2009). In contrast, their overlap is greater in larger settlements, possibly due to the prevalence of date orchards providing refugia from competitive interactions (e.g. Finke and Denno, 2006), and high resource abundance (e.g. Ochoa et al., 2021) – suggesting a mechanism of bottom-up control regulating predator communities (Newsome and Ripple, 2015). Foxes, the smallest of the predators, may be better able to share resources with wolves in settlements where jackals are suppressed (e.g. Kamler et al., 2003). Thus, both the distribution of predators and their interactions vary due to resource differences between agricultural settlements.

Geographic distributions of predators are tied to the increasing temporal availability of water resources between growing seasons. Predators further demonstrate distinct trends in their seasonal variation related to land-use practices of Kibbutz and Moshav agricultural habitats (Fig. 9). Around southern Kibbutzim, predators display patterns of peak seasonal occurrence during summer months (Fig. 9D–F), suggesting that predators exploit agricultural resource availability corresponding to peak water consumption requirements of date orchards during the hottest and driest months (Fig. 7), when environmental resources for wildlife are most scarce. Around northern Moshavim, wolves and foxes occur more evenly through the middle of the year (Fig. 9B and C), due to dissimilar agricultural crop regimes, namely pepper cultivation underlying seasonal agricultural water requirements (and availability to predators). However, around Moshavim these patterns show greater uncertainty especially during the summer season, indicating that native wolves and foxes might still be linked to natural environmental resource availability (Barocas et al., 2018). This may also reflect the heterogeneity in shifting agricultural land uses of privatized Moshav land parcels leading to seasonal fluctuations in species' use of different agricultural habitats (Guyot et al., 2017). Jackals have only recently begun to invade Moshavim, and due to significant increases in date orchard cultivation and their reliance on anthropogenic resources, we predict that here too they will occur seasonally more frequently as they become established. Our findings emphasize the season-specific implications of agricultural land-management choices and resource availability on animal distributions in dryland agro-ecological regions.

These trends in geographic and seasonal predator distributions and increased overall predator presence have had cascading trophic effects on gazelle prevalence and Acacia seed dispersal. Predators occur increasingly proximate to agricultural settlements (Fig. 3), which confirms similar findings on predator effects in the region in the vicinity of anthropogenic features and resource abundance (Shapira et al., 2008). Consequently, native desert gazelles adjacent to expanding agriculture have been displaced farther from settlements especially where predators are well established around Kibbutzim (median gazelle distance to Kibbutzim ranges from ~6 km in 2015 to 7 km in 2018; Figures A.5 & A.6). Gazelles play an important role in the dispersal, recruitment and germination (through digestive seed scarification) of Acacia, keystone vegetation critical to native desert species (Hackett et al., 2013). We showed that Acacia seedlings occur farthest from settlements (Fig. 10) and overlap strongly with gazelles (Figure A.7); a possible indication of the role of gazelles (and other large ungulates) in Acacia recruitment. Other native prey species in the region may similarly be threatened by intensive desert agriculture in a way that leads to the degradation of Acacia vegetation and desert ecosystems through cascading impacts (Ripple and Beschta, 2012) from the distributional expansion of predator species (e.g. gerbils, Shapira et al., 2008; and Arabian gazelles, Shalmon et al., 2019), and still newly invasive predators (e.g. stray dogs). Such cascading ecological effects due to agriculture and associated resource influxes are likely across dryland agroecosystems.

5. Conclusion

Agricultural management systems under different regimes influence landscape configurations, crop selection and water-use patterns in ways that not only affect land cover change locally, but also modify animal communities in surrounding areas resulting in cascading ecological impacts. Few studies incorporate contrasting crop management and resource factors impacting trophic cascades within an agricultural landscape, especially in resource-scarce dryland environments with acute and seasonal influx of agricultural-related inputs (e.g. Contos and Letnic, 2019). The novelty of our investigation lies in its incorporation of ecological trophic cascade theory to evaluate the role of agricultural regime differences underlying variation in landscape practices and resource inputs in modifying desert ecological systems. Our results have important implications for agricultural management and conservation in drylands due to large-scale agricultural land conversion. Drylands encompass a large part of the world's human-social and ecological environments (Reynolds et al., 2007), and are also among the most fragile and poorly represented ecosystems under current conservation schemes (Roll et al., 2017). Our findings suggest that agricultural development plans in arid regions should take into account the indirect effects of changing land-use strategies on surrounding ecological communities. In dryland systems, this could be done, for example, through measures mitigating invasive predator distributions and restricting their access to highly limited and seasonally fluctuating resources (e.g. water supply). Considering the rapid expansion of dryland agro-ecological systems globally, understanding and mitigating such socio-ecological cascading effects will become all the more crucial in the future.

CRediT authorship contribution statement

Amir Lewin: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Visualization, Funding acquisition. **Joseph J. Erinjery:** Conceptualization, Methodology, Formal analysis, Writing – review & editing. **Yann le Polain de Waroux:** Conceptualization, Writing – review & editing. **Effi Tripler:** Conceptualization. **Takuya Iwamura:** Conceptualization, Methodology, Validation, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

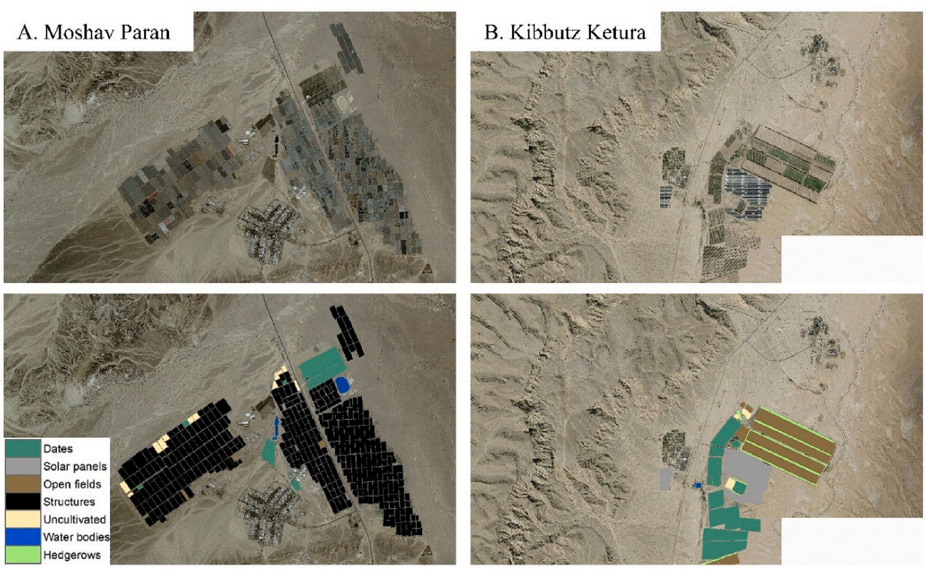

Fig. A.1. Semi-automated classification of agricultural land-use in the Arava Valley (2015), Israel using orthophotos (2 m resolution) from the Survey of Israel Mapping Centre (MAPI). (A) Moshav Paran (representative of Moshavim), in the north of the valley is dominated by net-houses and tunnels (i.e. closed structures). (B) Kibbutz Ketura (of the Yotvata settlement bloc, representative of Kibbutzim) in the south, comprises open fields and date orchards separated by hedgerows. Orthophotos were masked with a digital layer of delineated agricultural parcels from the Ministry of Agriculture (current as of 2016), used as a template to outline agricultural settlements by plot extents, and to separate general land classes in order to improve the quality of the supervised classification by avoiding similar land classes (e.g. open fields vs. native desert, green structures vs. date orchards). Each of these was then used separately during the supervised classification process, in which training data of specific land uses was compiled for the machine learning process. The classified products were then merged into one raster file with the following seven categories in the attribute table: date orchards, solar panels, open fields, structures, uncultivated fields, water bodies and hedgerows. The classification process was validated for accuracy assessment by visual cross-inspection using analogous higher resolution images (where available), and expert ground-truthing.

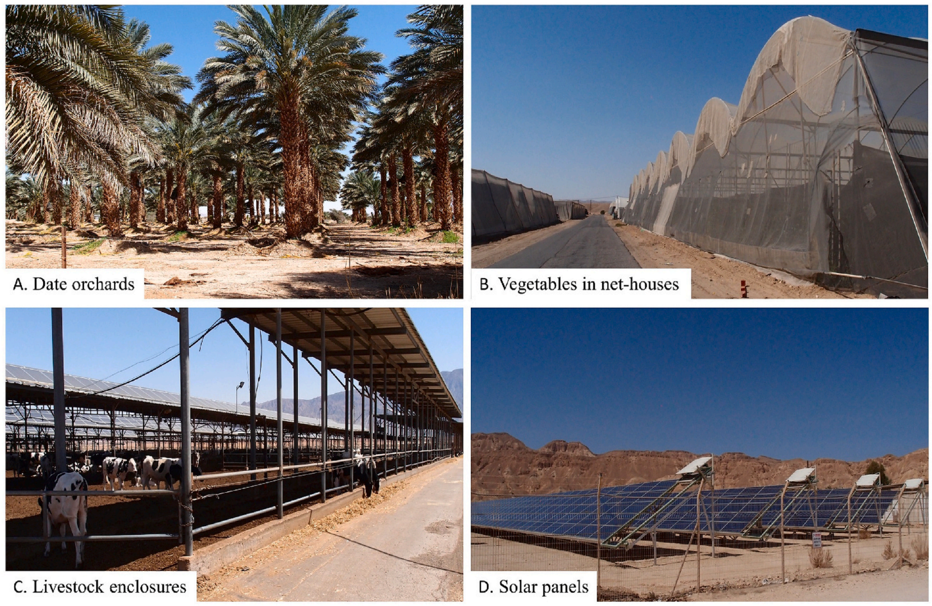

Fig. A.2. Photo images of major land-classes in the Arava Valley: A) Date orchards, B) Vegetables in net-houses, C) Livestock enclosures, D) Solar panels.

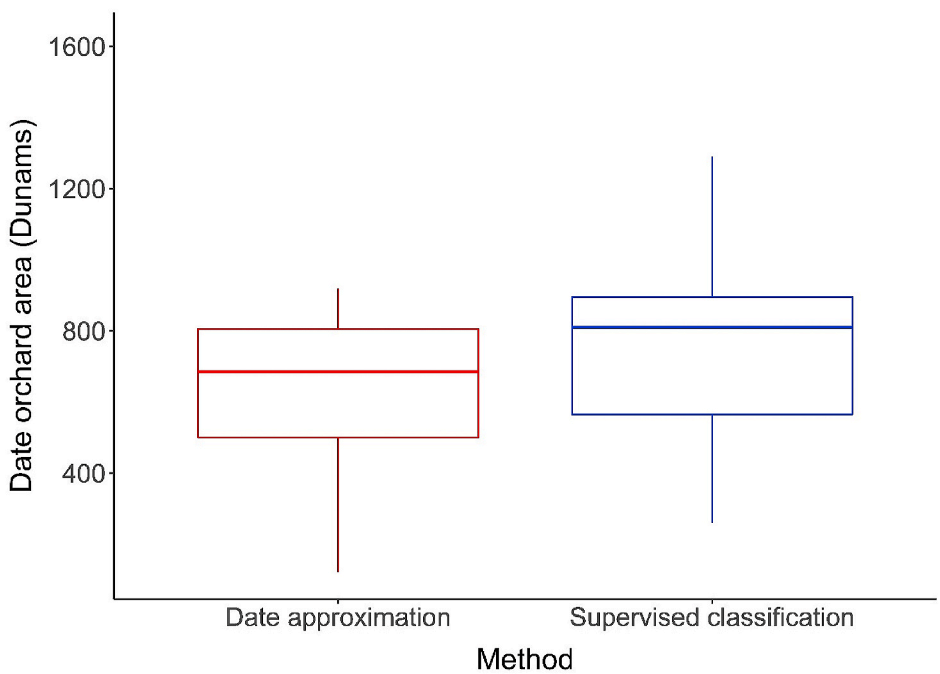

Fig. A.3. Welch's two sample *t*-test comparing approximation of date area and supervised classification method ($t = -0.32$, d.f. $= 29$, $p = 0.75$). To test the accuracy of our approximation of date orchard area (i.e. converting individual trees to area size), we compared these data to date orchard area calculated from the supervised image classification of aerial images (Figure A.1), to quantify the area of different land classes including date orchard area. We performed a Welch's two sample *t*-test to compare our approximation of date area to the supervised classification method and found that date area did not significantly differ between the two methods, therefore allowing us to validate the approximation of date orchard area used in our analyses.

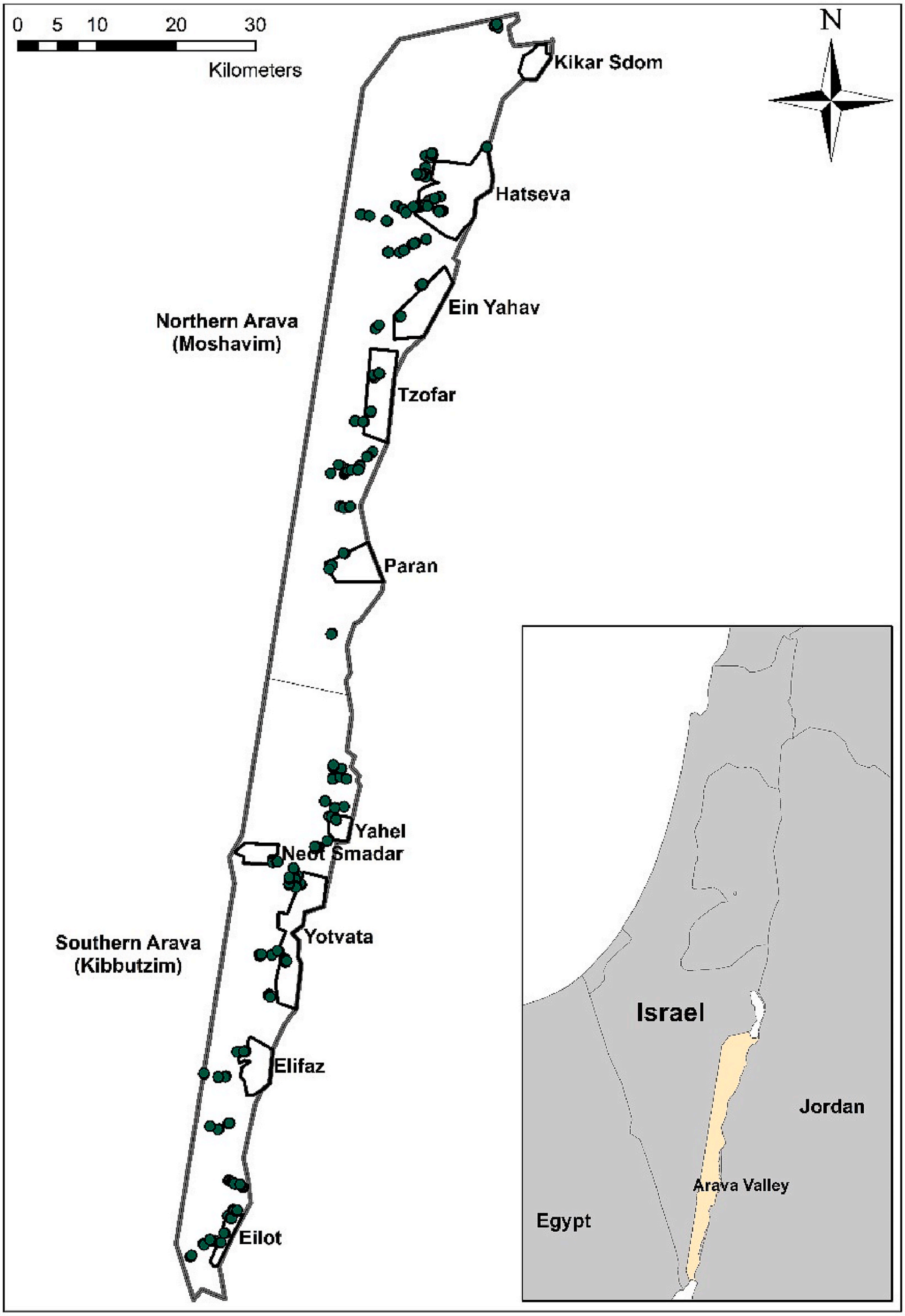

Fig. A.4. Map of the Arava Valley showing Acacia tree survey sites. Polygons equal agricultural settlement blocs in northern and southern regions (delineated by dashed line) of the Arava Valley, comprising Moshavim and Kibbutzim respectively. Green circles show Acacia tree locations from the 2013 Acacia Survey of the Open Landscape Institute (OLI).

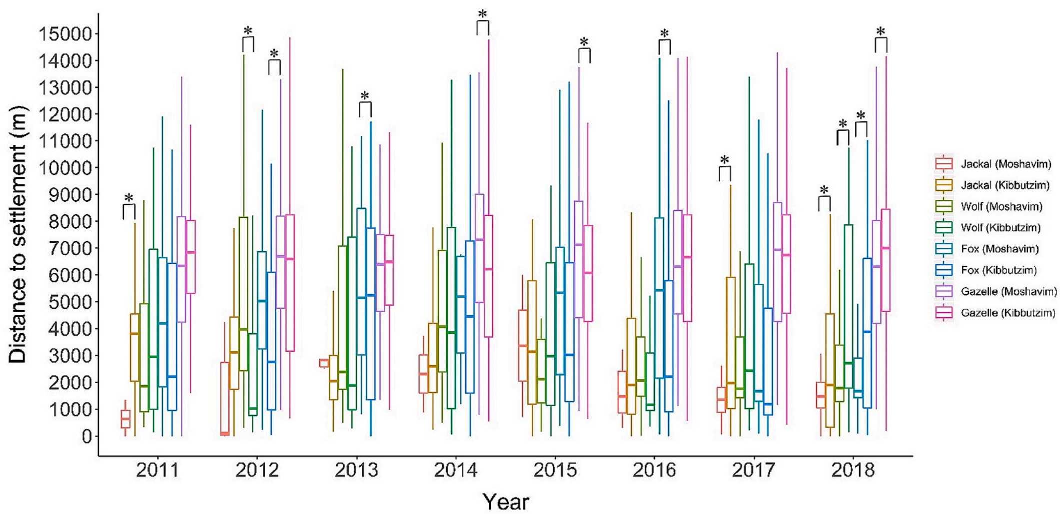

Fig. A.5. Differences in predator and gazelle species spatial proximity between Moshav and Kibbutz settlements from 2011 to 2018. Reds = jackals (*Canis aureus*), greens = wolves (*Canis lupus*), blues = foxes (*Vulpes vulpes*), purples = gazelles (*Gazella dorcas*). * denote significance using Tukey multiple comparisons of means within years, $p < 0.05$.

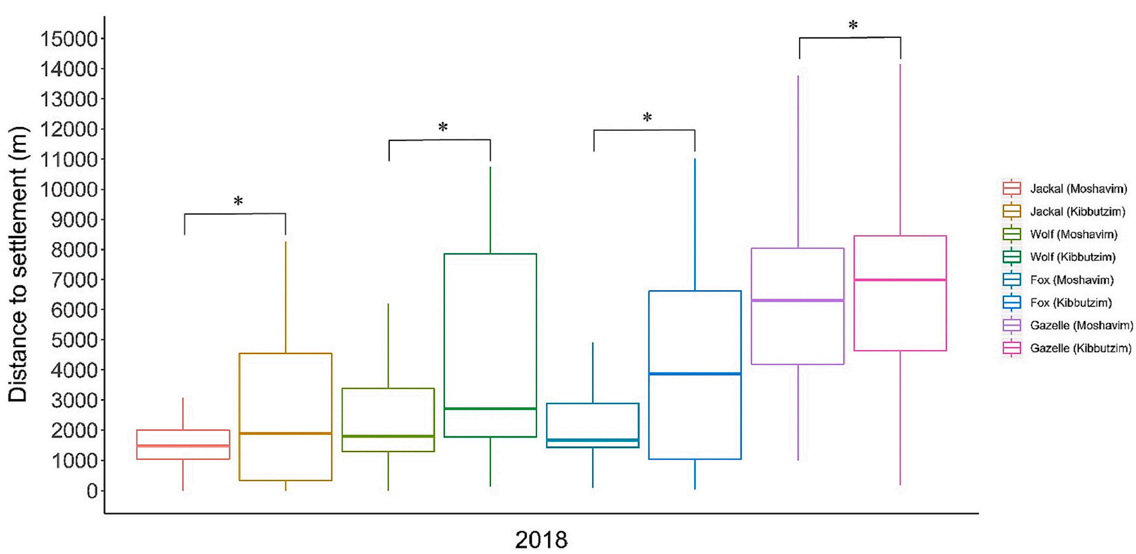

Fig. A.6. Differences in predator and gazelle species spatial proximity between Moshav and Kibbutz settlements in 2018. Reds = jackals (*Canis aureus*), greens = wolves (*Canis lupus*), blues = foxes (*Vulpes vulpes*), purples = gazelles (*Gazella dorcas*). * denote significance using Tukey multiple comparisons of means within years, $p < 0.05$.

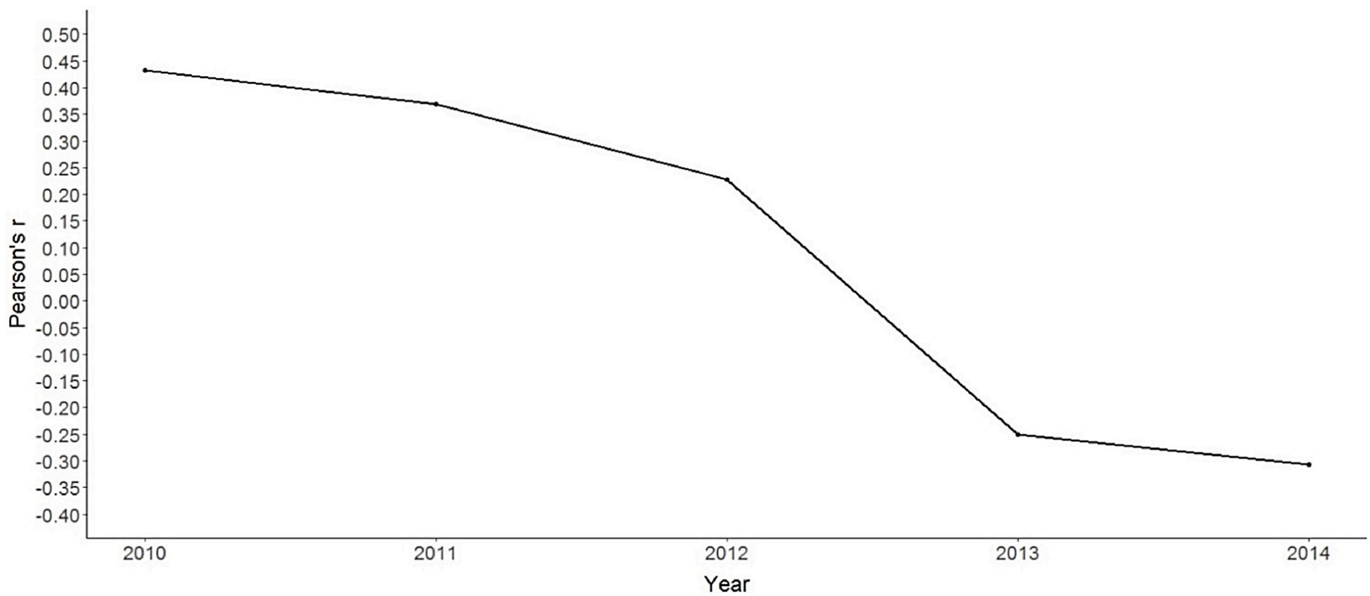

Fig. A.7. 0–2 m Acacia tree size category (representing seedlings) from year 2013 congruence (Pearson's Correlation) with yearly gazelle distributions (2010–2014). All values are significant, $p < 0.001$.

Table A.1
Goodness of fit measures from Generalized Linear Models in Fig. 8. Models are fitted sequentially, and columns give residual degrees of freedom, residual deviance, and $P(\chi^2)$ to test for significance.

Model	Model terms	Residual d.f.	Residual deviance	$P(\chi^2)$
Jackals (Moshavim)	Null	454	599.7	
	Water	453	596.4	0.06
	Dates	452	458.08	<0.001
	Vegetables	451	300.11	<0.001
	Livestock	450	296.81	0.07
Wolves (Moshavim)	Null	454	1872.8	
	Water	453	1738.5	<0.001
	Dates	452	1738	0.48
	Vegetables	451	1661.9	<0.001
	Livestock	450	1046.5	<0.001
Foxes (Moshavim)	Null	454	433.31	
	Water	453	411.88	<0.001
	Dates	452	411.01	0.35
	Vegetables	451	392.42	<0.001
	Livestock	450	385.36	<0.001
Jackals (Kibbutzim)	Null	444	2848.8	
	Water	443	2805	<0.001
	Dates	442	224.7	<0.001
	Vegetables	441	2161.4	<0.001
	Livestock	440	2021.1	<0.001
	Solar	439	2013.3	<0.001
Wolves (Kibbutzim)	Null	444	1233	
	Water	443	1172.6	<0.001
	Dates	442	1097.5	<0.001
	Vegetables	441	1094.6	0.09
	Livestock	440	1093.2	0.22
	Solar	439	1083.8	<0.001
Foxes (Kibbutzim)	Null	444	2604.7	
	Water	443	2468.7	<0.001
	Dates	442	2128.5	<0.001
	Vegetables	441	2112	<0.001
	Livestock	440	2030.8	<0.001
	Solar	439	2010.2	<0.001

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