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Increased songbird nest depredation due to Aleppo pine (Pinus halepensis) encroachment in Mediterranean shrubland

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Abstract

Background In recent decades, a decrease of passerine densities was documented in Mediterranean shrublands. At the same time, a widespread encroachment of Aleppo pines (Pinus halepensis) to Mediterranean shrubland occurred. Such changes in vegetation structure may affect passerine predator assemblage and densities, and in turn impact passerine densities. Depredation during the nesting season is an important factor to influence passerine population size. Understanding the effects of changes in vegetation structure (pine encroachment) on passerine nesting success is the main objective of this study. We do so by assessing the effects of Aleppo pine encroachment on Sardinian warbler (Sylvia melanocephala) nest depredation in Mediterranean shrublands. We examined direct and indirect predation pressures through a gradients of pine density, using four methods: (1) placing dummy nests; (2) acoustic monitoring of mobbing events; (3) direct observations on nest predation using cameras; and (4) observation of Eurasian jay (Garrulus glandarius) behaviour as indirect evidence of predation risk. Results We found that Aleppo pine encroachment to Mediterranean shrublands increased nest predation by Eurasian jays. Nest predation was highest in mixed shrubland and pines. These areas are suitable for warblers but had high occurrence rate of Eurasian jays. Conclusions Encroaching pines directly increase activity of Eurasian jays in shrubland habitats, which reduced the nesting success of Sardinian warblers. These findings are supported by multiple methodologies, illustrating different predation pressures along a gradient of pine densities in natural shrublands. Management of Aleppo pine seedlings and removal of unwanted trees in natural shrubland might mitigate arrival and expansion of predators and decrease the predation pressure on passerine nests.

Background

Alteration of natural habitat due to anthropogenic activities is the leading cause of biodiversity loss in terrestrial habitats (Newbold et al. 2015). Globalization has promoted alien species invasion to many parts of the world, thus threatening human livelihood and biodiversity (Early et al. 2016). Plants constitute for the majority of biological invasions worldwide and have tremendously impacted ecosystems (van Kleunen et al. 2015). Plant invasion changes habitat cover and structure, creating bottom-up cascading events with adverse effects on native species (Schirmel et al. 2016). Encroachment is a form of biological invasion, whereby native species spread to habitats from which they were historically absent.

In some cases, encroachment of native species to non-native habitats are a consequence of human actions or managements. For example, native conifer species encroachment to grassland, savannas and shrublands are a well-documented phenomenon across the globe (Richardson and Rejmánek 2004). In north America it is mainly attributed to lack of fire events due to human intervention, allowing conifers to expand and establish in low vegetation habitats (Davies and Bates 2017; Krannitz 2007; Livingston et al. 2016). Conifer encroachment changes both biotic and abiotic conditions in soils, native vegetation composition, diversity and densities of primary and secondary consumers (Bates and Davies 2017; Bombaci and Pejchar 2016; Coates et al. 2017).

Aleppo pine (*Pinus halepensis*), is a widespread species in Mediterranean forests (Richardson et al. 2000), but in the Mediterranean region of Israel, native populations inhabit relatively small and restricted areas on Mt. Carmel and the Judean mountains (Rabinowitch A 1985). Aleppo pines were planted in the early 20th century across Israel on over 100,000ha, and account for half of the planted forests in the state. Since then, a widespread encroachment of Aleppo pines into natural habitats has been observed across Israel (Lavi et al. 2005), mostly into Mediterranean shrublands (Osem et al. 2011). Whether Aleppo pine is now an invasive- or encroaching species in this region is still debated (Liphschitz & Biger 2001; Lavi et al. 2005; Rothschild 2018); we take a conservative approach and consider it encroaching, following Osem et al. (2011). Planted Aleppo pines produce seeds for approximately 30 years in the Mediterranean landscapes in Israel (Osem et al. 2011), and therefore, their impact on the floral and faunal structure is expected to continue. Hence, understanding the cascading effects of such changes is significant for understanding changes in the Mediterranean ecosystem of Israel.

Birds are considered sensitive to habitat change due to their specific adaptations to vegetation types, heights and densities (Brosh and Adam 2012; Shochat et al. 2002), and therefore they can be used as indicators of ecosystem intactness. Changes in vegetation structure may affect species' ability to seek shelter or cover from threats such as predators (Glasser and Hadar 2014). We studied the effects of pine encroachment in natural habitats on the presence of the Eurasian jay (*Garrulus glandarius atricapillus*), a common songbird nest predator (Schaefer 2004; Wegge et al. 2012), and the indirect effect of pine encroachment on Sardinian warbler (*Sylvia melanocephala*) nest predation. We hypothesized that avian predators such as the Eurasian jay may use pines as observation points to detect nests and that consequently pine encroachment will increase predation pressure.

The breeding season is a critical phase in the annual life cycle of birds, with important consequences to population growth and survival (Fuller et al. 1995; Gates and Gysel 1978; Ricklefs 1969; Yom-Tov 1974). Nest predation rates usually vary between 44% to 86% depending on habitat type and species (Martin 1988); vegetation structure (i.e., micro habitat) is a significant factor that may affect nest predation (Castro-Caro et al. 2014; Howlett and Stutchbury 1996; LaManna et al. 2015).

Pine encroachment to Mediterranean shrublands may have a similar effect to that of forest edges; edge effect is an ecological change that affects the community structure in the boundaries of the habitat (Murcia 1995). Forest edges can change resource availability for insectivorous birds (Holmes and Schultz 1988; Whelan 2001), as well as for nest predators; edges allow nest predators to forage in habitats other than their primary natural habitat (i.e., forest species forage in shrubland on forest edge). Increased nest predation is highly associated to edges of fragmented habitats (Batary and Baladi 2004), and is higher in clear edges like forest to agriculture.

There are several main predators of songbird nests in forested areas and shrublands. Small mammals (e.g. mice, rats) were found to be significant nest predators in forest habitats due to lower parental activity around the nest in such habitats (Weidinger 2009), as predatory bird species are more associated

with forest edges (Chalfoun et al. 2002). We hypothesized that avian predators will take advantage of spreading pines to natural shrublands in our study area.

Lahti (2001) suggested that nest predation probability can be determined by specific predator behavior (Lahti 2001). Members of the Corvidae family are known for their learning abilities and adaptive and opportunistic skills; therefore, these species are known to take advantage of forest edges to prey in low vegetation habitats (McCollin 1998; Piper and Catterall 2004). Long term monitoring through biennial bird surveys (by sound and vision along fixed transects) has been ongoing since 1985 (Brosh and Adam 2012). These surveys of the study area have shown an increase in Eurasian jay density and have led to our current study. Pine encroachment to natural habitats may increase edge effects thus promoting increased presence of avian predators, such as jays in the study area. Concurrent with an increase of jay density, long term surveys show a decrease in songbird nests. Here, we investigate nest predation pressure rates over a gradient of pine densities with different vegetation composition and height. Specifically, we address the following questions: 1) is there a correlation between songbird open nest predation and (a) pine density, (b) vegetation structure (c) predator community assemblage; 2) is there a correlation between nest predation pressure and presence and activity of jays.

Results

Egg predation in artificial nests

Over half of the 123 artificial nests (quail (*Coturnix coturnix*) and plaster eggs were pooled) were predated on (65 nests, 52.8%). The probability of nest predation was not equal among the four habitat types. Greatest predation (19.5 %) was recorded in the mixed shrubland and low-density pines and the lowest (7.3%) in dense pine plantations (Fig. 2).

Nest predator identification

Based on the 48 plaster eggs that we placed in artificial nests, we were able to identify four predator taxa according to marks left on 18 plaster eggs, (Fig. 3). The main predator group was medium size mammals (n=8), followed by rodents (n=7), birds (n=2) and reptiles (n=1) (*Pseudopus apodus*, Eurasian Glass Lizard). Some nests that were located close to the cattle corral disappeared completely with the shrubs around the nest site (n=3) (Fig. 3).

Our camera traps were set near artificial nests with quail eggs to learn about predator behavior: which predator species leave remains, which obtain all eggs, and which remove the entire nest. We found that jays were associated with 84% of documented predation events and 100% of those events ended up with eggs disappearing from artificial nests. A quarter of the nests (n=12) with quail eggs were emptied from all their eggs with no visible remains. Camera trap images showed that jays carried away the eggs, small mammals bit the egg and left remains in the nest and meso-carnivores removes entire nest. Therefore, artificial plaster egg disappearance was associated with avian predator category.

Predator assemblage was significantly different between natural shrubland (A) and the three other habitat types (Mixed shrubland and encroaching pines - *Wald value: 1.465, p < 0.01*; Low density Aleppo pine plantation - *Wald value: 2.122, p < 0.01*; High density Aleppo pine plantation - *Wald value: 1.733, p < 0.01*, Fig. 4). Avian predation was significantly higher in the natural shrubland mixed with pine than in natural shrubland, and avian predation in pine plantations was significantly lower than natural shrubland (intercept). Predation due to micro-mammals (i.e. rodents) occurred significantly more at mixed shrubland and mixed habitat and was not significantly different at the pine plantation habitat. Large mammal predation was significantly higher at low-density plantations and significantly lower at mixed shrubland and encroaching pines. Nest trampling due to cattle occurred significantly more at pine plantations than natural shrubland (intercept) (Fig. 4).

Nest survival probability

We estimated nest survival in relation to habitat type and the time within the breeding season (March, April and May). We used natural shrubland as an intercept. The GLM binominal distribution model predicted that nest survival probability was significantly lower in the mixed shrubland and encroaching pine during the whole breeding season in comparison with the other three habitat types (*coeff: -1.6814 (SE0.58), p = 0.016*). The probability of survival was also low in the low-density pine plantations; however, this difference was not significant in comparison to the natural shrubland (*coeff: -0.7845 (SE0.53), p = 0.14*) (Fig. 5). The probability of survival was relatively high but not significantly different between the two control habitats, natural shrubland and high-density pine plantation respectively) (*coeff: -0.4560 (SE0.5), p = 0.42*). Time within the nesting season (measured by month) had a significant impact on nest survival where nest was more likely to survive in the beginning of the nesting season (March) than later in the season (April and May). Lowest survival predictions (compared to March (intercept)) were estimated in April (*coeff: -1.3901 (SE0.47), p = 0.003*), followed by May (*coeff: -0.9354 (SE0.52), p = 0.072*) (Fig. 5).

Indirect evidence of predation pressure

Sardinian warbler mobbing calls represent the extent of “threat” in a given habitat and Eurasian jay calls represent predator presence in a given habitat. We analyzed 220 hours of recordings from 16 different plots. We found that the number of Sardinian warbler mobbing calls was significantly different among the four habitat types (*Kruskal-Wallis, χ^2= 15.564, df=3, p = 0.0014*). Post-hoc with Wilcoxon tests and Bonferroni correction showed significantly lower number of mobbing calls in the natural shrubland in comparison to the other three habitats. The highest number of mobbing calls was detected in the mixed shrubland and pine plantation habitat (Fig. 6).

Although the number of jay calls, identified from the acoustic monitoring, was not significantly different between the four habitat types (χ^2 =6.888, df = 3, P= 0.076), the results showed higher numbers in the mixed shrubland and in the low-density pine plantation and lowest number of calls in natural shrubland.

Direct observations

Direct observations on fixed trails were carried out 20 times throughout the study. We recorded 67 jay occurrences in the study area and characterized them to three types of activity: (1) foraging; (2) flying; (3) observation points. We used a multi-dimensional analysis based on a GLM framework to distinguish between activity occurrences between the four habitat types. We used natural shrubland as an intercept in the model, thus the three other habitats were compared to this habitat and were found to be significantly different in terms activity type assemblage (Mixed shrubland and encroaching pines; *Wald value: 2.956, p value = <0.005*); (Low density Aleppo pine plantation; *Wald value: 1.717, p value = <0.005*); (High density Aleppo pine plantation; *Wald value: 2.844 p value: <0.005*). We assessed goodness of fit using Likelihood Ration Test and Akaike information criterion (AIC) score, model that included habitat performed better (Jay Behaviour ~ Habitat; AIC = 69.6; Null (Intercept only): *AIC = 70.83; LRT = 16.773, $p(\chi^2) = 0.05$*). Significantly increased foraging behavior and decreased flying behavior were observed at all three habitats in comparison to natural shrubland and was positively correlated to mixed shrubland and pines (Fig. 7). Jays were also observed significantly more on observation points in these three habitats in comparison to the natural shrubland (Fig. 7). These results indicate that jays flew over more frequently in natural shrubland without stopping to forage in this habitat.

Discussion

We found that Aleppo pine encroachment to natural shrublands increased nest predation events by Eurasian jays due to changes in habitat structure. Our results highlight how encroaching pines can directly increase the activity of avian predators in shrubland habitats and reduce the nesting success of shrubland songbirds. These findings were based on multiple methodologies that illustrated different predation pressures among the four habitat types, including artificial nest predation, acoustic monitoring of warbler mobbing events and jay calls, and jay activity patterns in relation to a gradient of pine densities in natural shrublands.

A 30-year long term songbird nesting survey (1985-2015) carried out in this study area has demonstrated a decline in warbler and some other passerine densities, and an increase of jay densities (Brosh and Adam 2012). Results of our study offer a mechanistic explanation for this decline. We expect that increased nest depredation due to forest encroachment affects other shrubland passerines that have a similar breeding strategy to that of the Sardinian warbler. Further investigation is needed to assess this hypothesis. Changes in species densities and species turnover along vegetation gradients have been linked to predation pressure (LaManna et al. 2015). In habitats that undergo rapid changes, like in cases of biological invasions (Dogra et al. 2010), such changes may therefore be accelerated. We found that decrease of songbird species in areas of tree encroachment is not a direct response to vegetation change but to increased predation. The lack of parental activity around artificial nests may lower the probability of detection by predators (Martin et al. 2000), so the results we present here may underestimate the predation risk to active nests.

Birds from the Corvid family detect nests more efficiently by using elevated points such as electricity poles to observe nesting areas (DeGregorio et al. 2014). In the current study, it is encroaching trees that

serve jays for the same purpose. Eurasian jays do not forage far from forest patches (Andren 1992; Shochat et al. 2002) and our results concur; we found a high presence of jays in pine-encroached shrublands and in pine plantations, and a lower occurrence in undisturbed shrublands. Previous studies found that nest predation in open landscapes and shrublands decreased with increasing distance from forest edges (Masoero et al. 2016); our results provide a mechanistic explanation to such observations.

Conifer encroachment into shrublands can facilitate prey bird movement via "stepping stones" that the pines create (Welstead 2002). Also, tree vantage points within the landscape reveal the passerine activity around the nest for jays and in mixed shrubland and pine patches. Schmidt (1999) suggested in a theoretical paper to look at nest predation from an optimal foraging theory perspective. It predicts that nest predators would forage where they have the best energetic profit to their foraging efforts (Schmidt 1999). We suggest that Eurasian jays may profit by foraging more efficiently using vantage points on pine trees.

Conclusions

In the last 150 years, the distribution of woody vegetation in open habitats, such as grasslands and savannas, has increased worldwide, jeopardizing biodiversity (Browning et al. 2008). Our study demonstrates that the encroachment of Aleppo pines into shrubland habitats may promote Eurasian jay populations and those of other avian predators, and consequently negatively impact populations of open-nest passerines. Thus, our results illustrate a causal mechanism of changes in bird community, which is generalizable to other parts of the world that suffer from tree encroachment. In areas of encroachment of encroaching pines, such as the Mediterranean region, measures should be taken to control this phenomenon. A first measures would be to cease planting conifer forests for recreational use. Second, management of seedlings at existing plantation edges. Third, removal of mature encroaching trees from natural shrub habitats. We encourage land and wildlife managers to consider our conclusions for decisions in conservation management schemes of passerine populations.

Methods

Study Area

The study was carried out in Ramat Hanadiv Park in the southern Mt. Carmel, Israel (32° 30' N, 34° 57' E), an area of 450 ha, surrounded by suburbs and agricultural fields. A cultivated memorial garden is located in the park center. The area is a plateau with a mean elevation of 120 m above sea level. The climate is typical Mediterranean with an average maximal temperature of 25.6 °C and minimal temperature of 16.4 °C, the average wind speed archives 9.78 m/s, rainfall averages 493 mm annually, and occurs mainly from November to March (Meteorological weather station data. http://www.meteo-tech.co.il/hanadiv/hanadiv_periodical.asp# ; Accessed 12 Nov 2019). The main vegetation structure is an open shrubland with broad-leaved phillyrea (*Phillyrea latifolia*) and mastic tree (*Pistacia lentiscus*) and

planted groves of Aleppo pine (*Pinus halepensis*), Turkish pine (*Pinus brutia*), and stone pine (*Pinus pinea*) (Hadar 1989).

Study design

We chose four different habitat types that differ in pine densities and height as well as in vegetation cover and composition (Table 1, Fig. 1): (1) Shrubland: an open shrub with mainly broad-leaved *P. latifolia* and *P. lentiscus*, without trees that taller than 3 meters. Annual and perennial herbaceous plants occur between the shrubs; (2) Mixed shrubland with pines: an open shrub of *P. latifolia* and *P. lentiscus* with Aleppo pine trees taller than 3 meters (10-15 trees per hectare). Annual and perennial herbaceous plants occur between the shrubs and trees; (3) Low density pine plantation: a mixture of pine and mastic shrubs. Annual and perennial herberous vegetation occurs between the shrubs. Density of 30-40 trees per hectare; (4) High density pine plantations are characterized by densities of 70 - 80 trees per hectare. Some Cypress trees (Cupressaceae) and few Mastic tree. We consider trees that are taller than 3 meters based on Light Detection and Ranging (LiDAR) data products provided by Ramat Hanadiv. We used habitat types 1 and 4 as controls: the shrubland is a typical warbler habitat and the high-density pine plantation is a typical habitat of the Eurasian jay. Jays are highly intelligent birds that use their learning abilities (Emery and Clayton 2004; Shaw et al. 2013) to specialize in nest robbing, particularly in forest edges (i.e., mixed shrubland and pines). In each habitat we quantified predation pressure using three methods (detailed below): (1) artificial warbler nests to monitor nest survival and predator community; (2) monitored warbler mobbing events and jay calls using acoustic recordings to assess predation pressure and jay presence; and (3) direct observations on jay activity; (4) validation of predator events using camera traps (Fig 1).

Artificial nests

We randomly chose 16 study plots (4 for each habitat) of 0.2km^2. Four dummy nests were randomly stationed in each plot, 30-100 meters apart, in two breeding seasons (2015 and 2016). The nests were built from local weeds, flax and Raffia palm fibers in diameter of 10-15cm in a coiling basket wreathing method (Paul Shaw 2009). The size and the material of the nests were made after examining Sardinian warbler nests from the Steinhardt Museum of Natural History (Tel Aviv University, Tel Aviv, Israel) nest collection. We placed two types of eggs in these artificial nests: (1) Quail (*Coturnix coturnix)* eggs that were boiled in order to postpone their rotting; (2) 3D printed plaster eggs similar to the size and decorated texture of Sardinian warbler eggs (model Projet® CJP 660Pro by 3D Systems) (Venuvinod and Ma 2004). The artificial eggs were covered with white bee wax and mixed with droppings from a chicken (*Gallus gallus domesticus*) to mask the smell of wax. The wax was used to collect information on nest predators according to the marking left on eggs (e.g., teeth and beak marks). Each nest was placed in the thickest shrubs in each plot and was reinforced to bush branches with a zip tie at a height of 50-120 cm from the ground, similar to the natural nesting sites of Sardinian warblers (Shirihai et al. 2001).

Three boiled quail eggs were placed in 80 nests (16 nests in each cycle) in five different cycles (18th April to 3rd May 2015, 15th May – 5th June 2015, 1st to 22th March 2016, 10th to 30th April 2016, 6th to 27th June 2016). Each nest was set in the field for three consecutive weeks. Three plaster eggs were placed in each nest in the three experiment cycles during 2016 breeding season (1st to 22th March 2016, 10th to 30th April 2016, 6th to 27th June 2016). Five nests fell off the shrub and were lost, leaving a total of 43 nests in these experiments. Each nest was set in the field for three consecutive weeks. Predation marks on the eggs were identified to species level by measuring incisors of the common rodent species and canines of common carnivores. For reptiles, we compared bite marks with preserved specimens in the Steinhardt Museum of Natural History skull collection. Avian marks were identified by beak and claw marks as described on acorns in birds tracks and sings field guide (Elbroch et al. 2001).

The association between predator assemblage and habitat type

We used a multivariate abundance model based on a generalized linear model (GLM) (Wang et al. 2018) to correlate between the predator assemblage and the habitat type. This high dimensional GLM analysis has been proven to have better power than common distance-based methods (Wang et al. 2012), and enables to make hypotheses about community-environment associations (both community-level and taxon-specific inferences), and estimates the direction and influence of explanatory variables have on single species and a whole communities, Model selection was conducted using a stepwise procedure and nested models were assessed by Likelihood Ratio Test and AIC score. The analysis for all taxon levels was done using 'mvabund' package (Wang et al. 2012) available on R (R Core Team 2015).

Nest survival probability

We modeled the probability of nest survival with a binominal generalized linear model (GLM) using the "stats" package in *R* v3.2.3 (R Core team 2015). First, we compared predation rates upon the plaster and the quail eggs and found no significant difference using Chi square with Monte Carlo simulation (due to the small sample) (*n= 123, df = 3, p=0.86).* Therefore, the experiments with the two types of eggs were pooled prior to the GLM analysis. Model explanatory variables were: 1) four habitat types (categorical); 2) pine density within a buffer of 50 meters around each nest; 3) land cover (vegetation, ground, rock cover) classified by a random forest model using RGB aerial image 7 cm^2 resolution; 4) mean vegetation height within a 50-meter buffer based on Light Detection and Ranging (LiDAR)(Bar Massada et al. 2012); 5) the month that the nests were placed (categorical). Best model was chosen using multi-model inference based on AIC scores.

Indirect evidence of predation pressure

We used acoustic monitoring to document mobbing calls of Sardinian warblers and recorded Eurasian Jay calls in the four habitat types as indirect indication for predation events. Preliminarilty assessment showedthat the detection range for Sardinian warbler calls was 50 meters from the device. Jays are detected by sound from 200m during bird count surveys (Brosh and Adam 2012), so we assumed they would be readily detected from 50m. We recorded ambient sounds in 16 plots (four of each habitat type)

for five consecutive days from mid-March to May 2015 and 2016. The recordings were made using a mobile recording device (TASCAM model DR-07 MKII; Made in Japan). Because we deployed unused devices of a single model, we expect that the variation among devices is minimal, and did not calibrate our microphones prior to the study. Additionally, our sound data was not used for spatial analysis, which may be biased by differential detection range, but only for species classification, which is based on the signature of sound rather than its magnitude. The recorders were placed in the first two hours of daylight and recorded at least six hours of omnidirectional sound. The recording parameters were made at a 16-bit rate and 44.1kHz. The acoustic analysis was conducted with Raven Pro 1.5 software from the Cornell University Bioacoustics lab (Bioacoustics Research Program 2014). The spectrogram parameters for mobbing calls detection was made in a 592-window size and with 80% overlap in window method Hann. Hann method is a form of smoothing of the sound signal. It raises the cosine curve so that its minima just touch zero. This is done prior to any sound analysis in order to reduce spurious “sidelobes” that appear at frequencies flanking each analysed frequency in a spectrum (Berryman et al. 2004; Podder et al. 2014; Wickramarachi 2003).

The Sardinian warbler alarm calls are typically made from repeating tk-tk-tk-tk notes (Shirihai et al. 2001). To detect these mobbing calls automatically we created a detector with the Raven software to detect the single notes of the mobbing calls in the frequency range of 4500 to 6000 Hz duration of 0.01-0.04 seconds with a minimal time interval of 0.008 seconds. We used *R* (R Core team 2015) to locate sequences of 20 notes or more (i.e., warbler mobbing sounds) counted all the mobbing calls within a 20-minute interval as a single mobbing event. For Eurasian jays we built a detector in frequency range of 1000 to 6000 Hz duration of 0.3-0.5 seconds with a minimal time interval of 0.5 seconds. All the automated selections were scanned by hand for any mistakes of the algorithm. In total, we scanned 220 hours of recordings. We conducted Kruskal-Wallis test with the *stats* package (R Core Team 2015) to find if the number of mobbing events per two hours was significantly different between the four habitat types.

Direct observations

During the two nesting seasons, we conducted direct observations along 10 trails in the first two hours of the morning in each of the four habitat types. Transects were conducted along fixed 2.5-3 km trails. The transect crossed each vegetation type where artificial nests were placed. Observations were done with a binocular. Transect counts were repeated 8 times throughout each season at 1-week intervals (mid March-May 2015-2016). We recorded Eurasian jay presence and described its activity (e.g., flying, foraging, observing). We used a multivariate abundance model based on a generalized linear model (GLM) to correlate the activity type and habitat type. We assessed goodness of fit using Likelihood Ration Test and Akaike information criterion (AIC) score. We performed a power test analysis to assess the strength of the model. Based on our simulation a minimum of 37 counts are needed to model jay occurrence in relation to observed behaviour and habitat type (simulated degrees of freedom: 26.51; simulated effect size: 0.81 [based on 0.45 of explained variance]; alpha = 0.05; power = 0.95). Analysis was conducted using the *pwr.f2.test* function from ‘pwr’ package available on CRAN (Champely et al. 2018).

Direct evidence of predation with camera traps

We placed 48 camera traps (Bushnell Trophy cam 8MP and 24 Bushnell Trophy cam HD, USA) next to 48 artificial nests with quail eggs for a period of three weeks (dates) to directly document predators and predation events behavior. Each camera was stationed next to artificial nests. The cameras were placed 1 - 1.5m away from each nest. A previous study showed that the cameras do not bias breeding success (Herranz et al. 2002). Camera trap photos were examined visually to confirm identification of the marks found on plaster eggs. Photographic data was not analyzed further than that because we did not place cameras at every nest.

List Of Abbreviations

1. Akaike information criterion (AIC)
2. Light Detection and Ranging (LiDAR)

Declarations

Ethics approval and consent to participate: Not applicable

Consent for publication: Not applicable

Availability of data and material: Data collected for this study is stored at and can be requested from Ramat Hanadiv Nature Park.

Competing interests: There are no competing interests.

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Authors' contributions: ABD and HS are first authors and contributed equally. ABD, HS, RE, RM, TD, II contributed to the idea, and design of the study. ABD, HS, RE, RM, TD, II contributed to the writing. ABD, HS, RE, RM analyzed the data. All authors read and approved the final manuscript. TD, II co-supervised the work presented here.

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Table 1

Table 1. The properties of the habitat types in Ramat Hanadiv Nature Park (following Bar Massada et al. 2012).

Habitat type	% of the park area	Typical plants	Structure
Natural shrubland	35 %	Broad-Leaved Phillyrea, Mastic tree.	0.5–2 m tall, 25–50% cover
Mixed scrubland with pines	31%	Broad-Leaved Phillyrea and Mastic tree and few pine trees.	0.5–5< m tall, >75% cover
Open pine plantation	4%	Pine trees with Mastic tree.	height > 5 m, <75% cover
Dense pine plantation	7.4 %	Pine and Cyprus trees.	height > 5 m, >75% cover

Figures

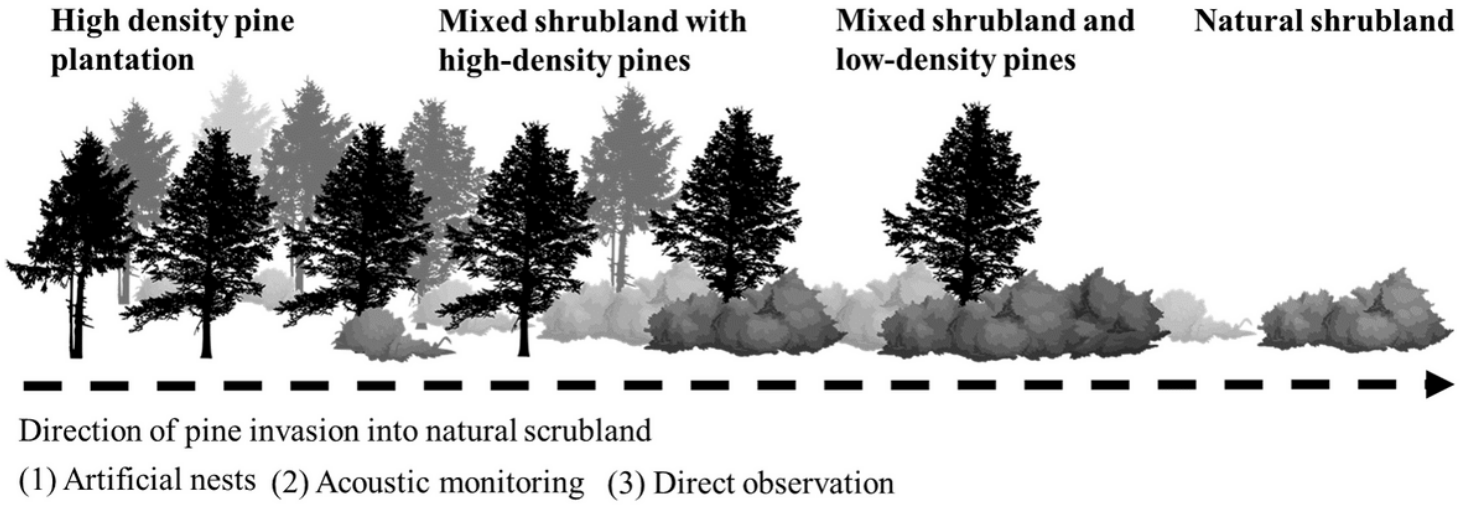


Figure 1

Conceptual figure of study design. Four habitat types following a gradient of pine densities: A) natural shrubland; B) mixed shrubland and low-density pines; C) mixed shrubland with high-density pines; D) high density pine plantation. In each habitat, be used three methods to monitor predation pressure and warbler and jay occurrence (artificial nests, acoustic monitoring, and direct observations).

Figure 2

Artificial nest location at the study area, Ramat Hanadiv Nature Park, Israel. Monitoring March-May 2015-2016. Predated nests (red), saved nests (light blue). Habitat type: A shrubland, mixed scrubland and pine trees, low density pine plantation, high density pine plantation.

Figure 3

Plaster egg with teeth marks of: (1) white-breasted hedgehog (Erinaceus concolor) -clear mark of the canine; (2) different rodents (marks of the insectivores especially on the tip of the egg), marks of an avian predator; (3) triangle marks of bird's nails.; (4) triangle marks of a wide beak and teeth marks by a European Glass Lizard (Pseudopus apodus); (5) marks of row symmetric teeth similar in size.

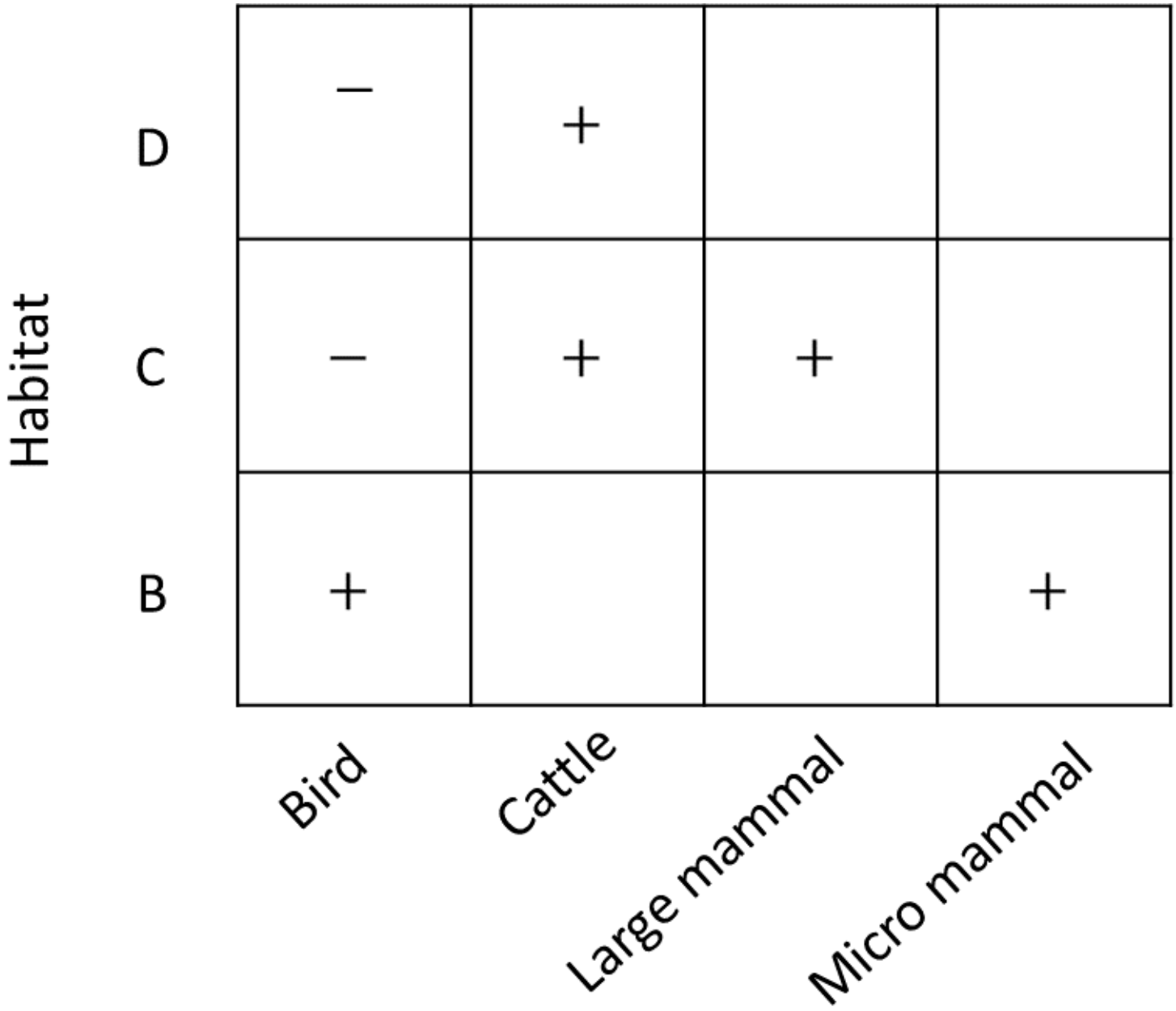


Figure 4

Individual predator type response to habitat type tested using a multivariate abundance model based on a generalized linear model (GLM) from data obtained by artificial plaster egg experiment. Presented are coefficient response with significance ($p<0.05$) in comparison to intercept – habitat (A). Habitat type: (A –

intercept) Natural shrubland; (B) Mixed shrubland and invasive pines; (C) Low density Aleppo pine plantation; (D) High density Aleppo pine plantation. Positive correlation (+), negative correlation (−).

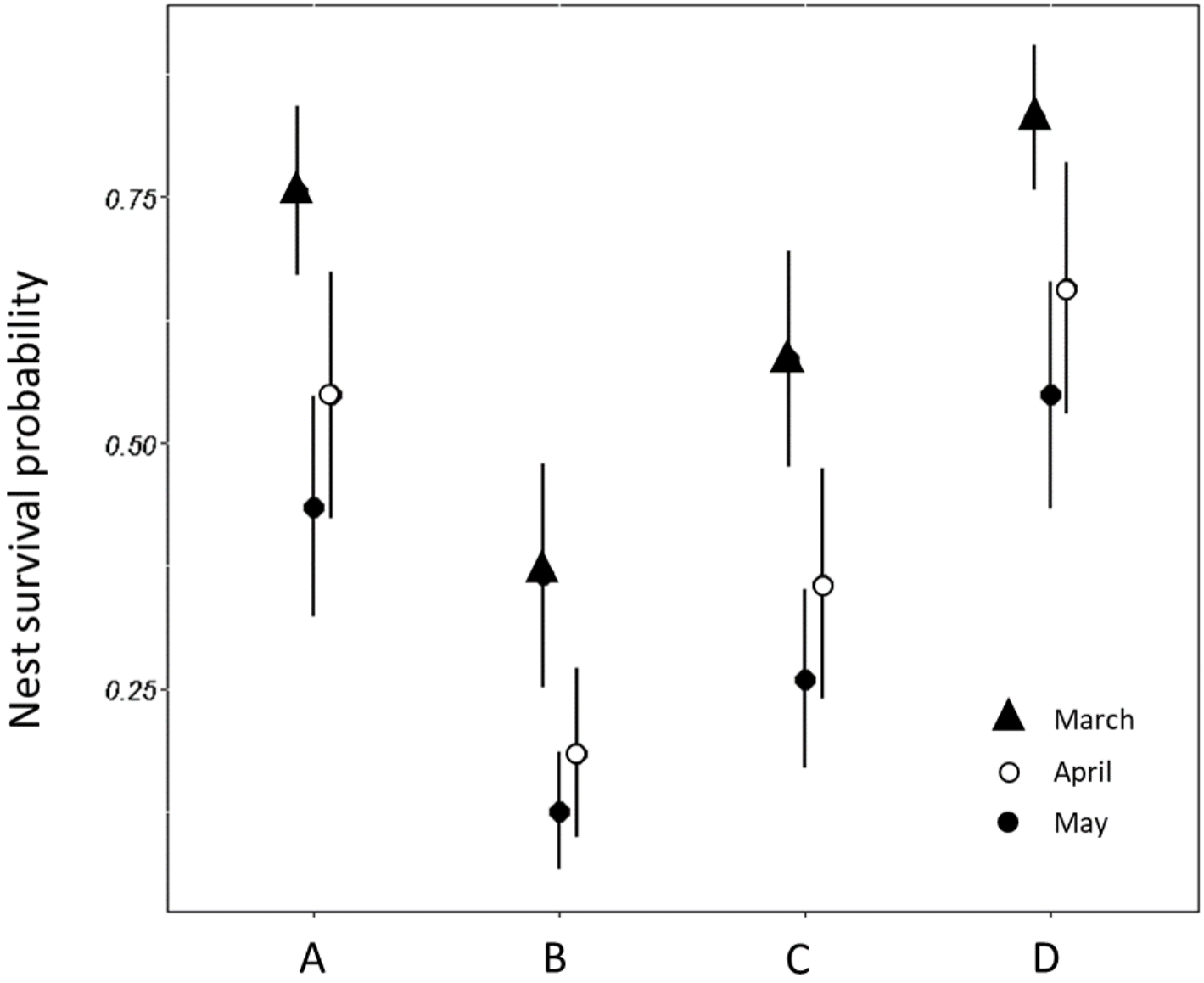


Figure 5

Predicted estimation of the nest survival probability in relation to habitat type and time of nesting season (month: March (triangle), April (hollow circle), May (full circle)). Whiskers indicate lower and upper confidence intervals. Habitat types: (A) Natural shrubland; (B) Mixed shrubland and invasive pines; (C) Low density Aleppo pine plantation; (D) High density Aleppo pine plantation. Data collected at Ramat Hanadiv Nature Park during March-May 2015-2016.

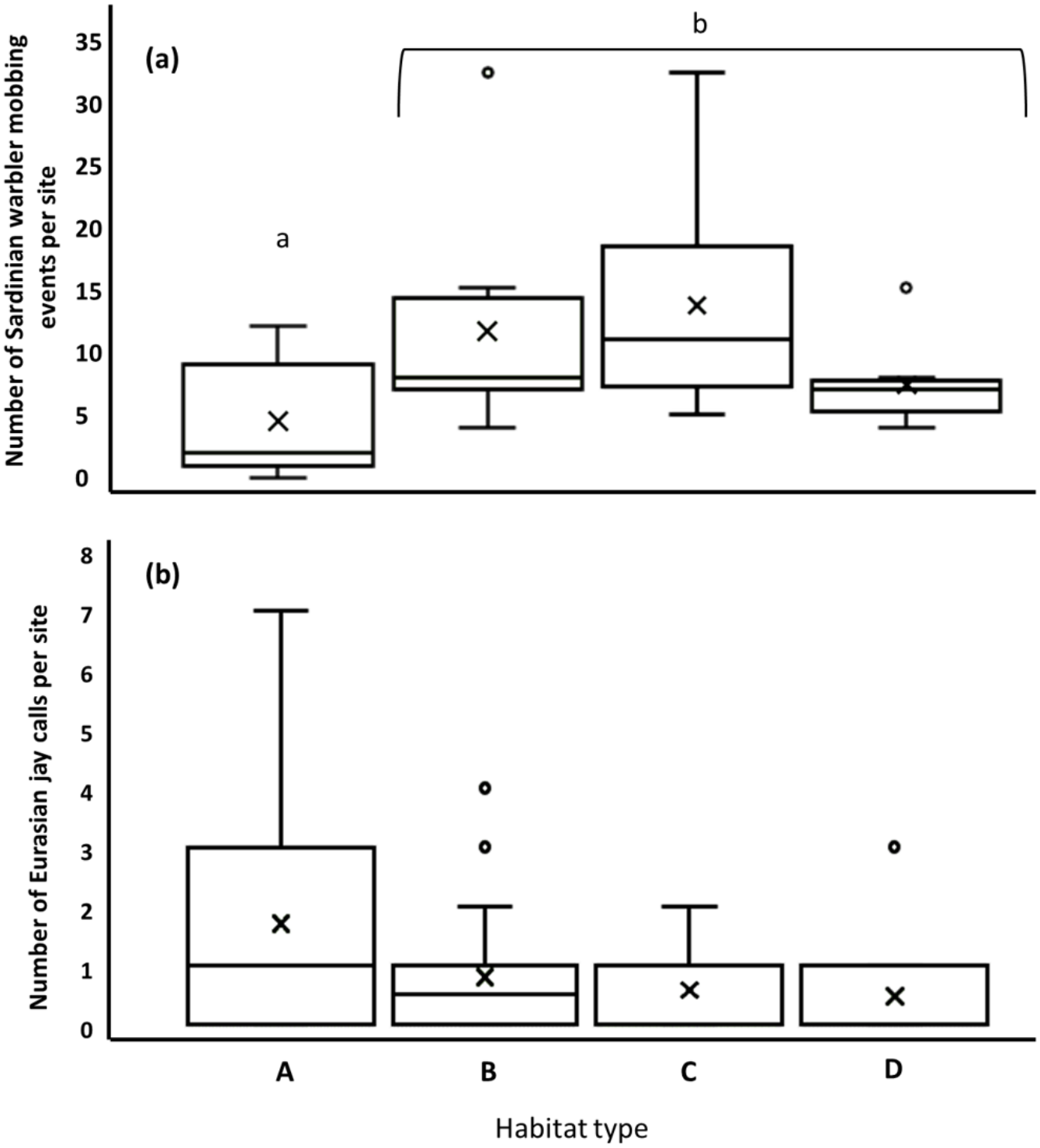


Figure 6

Sardinian warbler mobbing events (a) and Eurasian jay calls (b) in the four habitat types: natural shrubland; mixed shrubland and encroaching pines; low density Aleppo pine plantation; high density Aleppo pine plantation. The distribution of Sardinian warbler mobbing events (mean (×), median (solid line), post-hoc difference (letters A, B), whiskers represent upper 0.95 and lower 0.05, box upper 0.75 and lower 0.25. Points represent outliers. Based on 220 hours of recordings from 06:00-10:00 AM (n=88). Habitat types: (A) Natural shrubland; (B) Mixed shrubland and encroaching pines; (C) Low density Aleppo

pine plantation; (D) High density Aleppo pine plantation. Data collected at Ramat Hanadiv Nature Park during March-May 2015-2016.

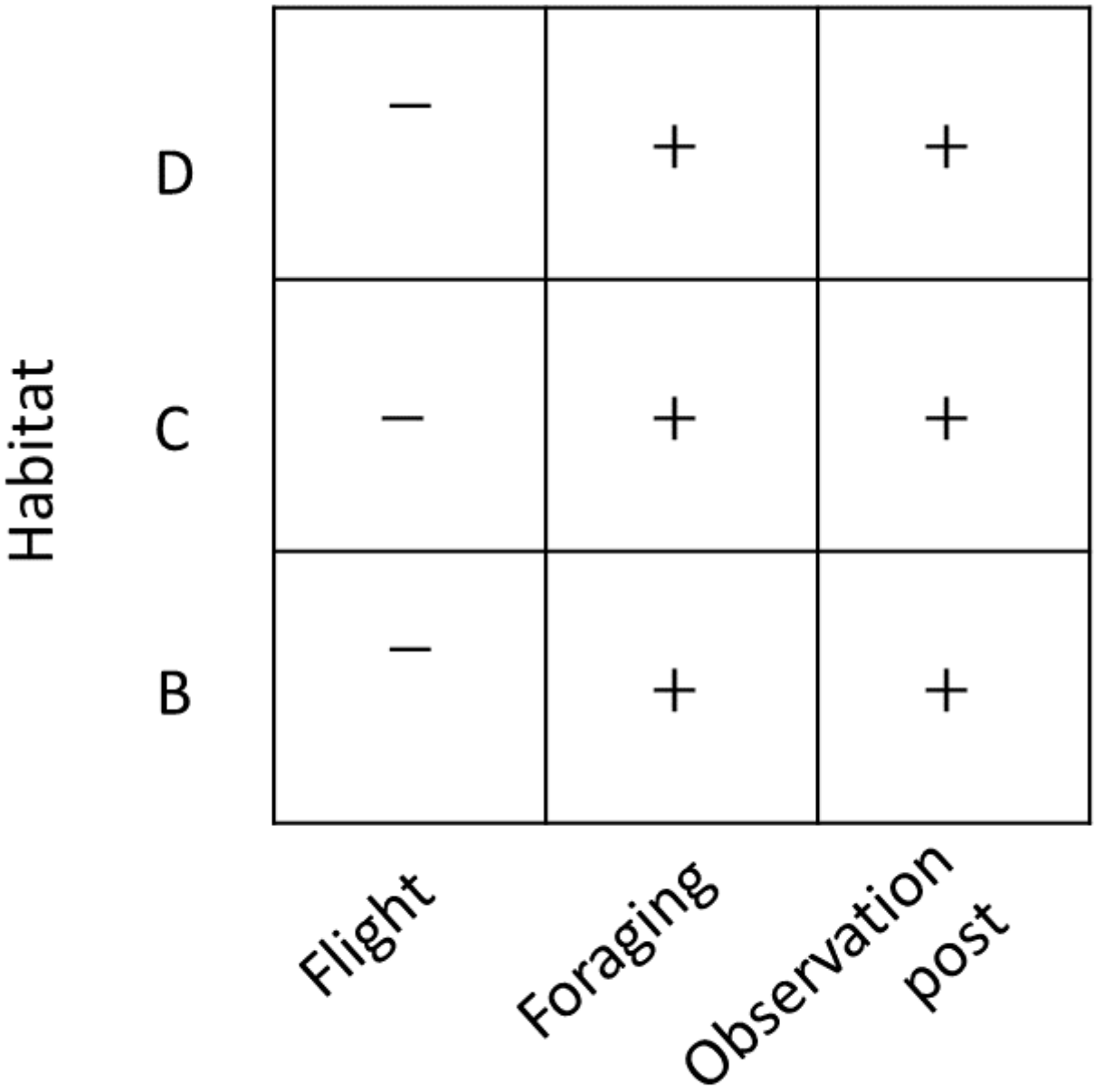


Figure 7

Activity type correlation to habitat type. Activity: (1) foraging; (2) flying; (3) siting on observation points (trees). Presented are coefficients with significance ($p<0.05$) in comparison to intercept – habitat (A). Habitat type: (A – intercept) Natural shrubland; (B) Mixed shrubland and invasive pines; (C) Low density Aleppo pine plantation; (D) High density Aleppo pine plantation. Positive correlation (+), negative correlation (−).