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# Understory vegetation in planted pine forests governs bird community composition and diversity in the eastern Mediterranean region

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## Abstract

**Background:** Managed forests can become a seminatural habitat by allowing natural vegetation to establish under the tree canopy. The aim of this study was to examine how this natural understory vegetation in pine plantations affects bird community composition and diversity. We compared bird communities in three types of pine forest plantations that differed in the composition of their understory vegetation.

**Results:** One thousand four hundred seventy-six birds of 33 species were observed in the three different forest habitats over two years. We found that the presence and composition of understory vegetation had a major role in determining bird community composition, richness, complexity and diversity.

**Conclusions:** To ensure pine forest with high biodiversity in the eastern Mediterranean region, the understory needs to be rich in shrubs that are attractive to birds and other natural fauna.

**Keywords:** Pine forest, Plantation, Understory, Vegetation, Birds, Community composition, Diversity, Habitat structure

## Background

### General

Seven percent (98,600 ha) of the state of Israel is covered by managed forests, whereas only 1.3% (18,500 ha) is natural woodlands (CBS - Statistical abstract of Israel 2014; JNF 2014). More than one third (35%) of the managed forests were planted before 1970 and 36.1% (40,700 ha) of them are stands of pines and mixed pine forests (JNF 2014). Managed coniferous forests differ markedly in their understory vegetation: whereas some forests may be bare of vegetation, other stands of the same age can be rich in shrubs and climbers (Ne'eman and Izhaki 1999; Dufour-Dror 2005; Fuller et al. 2007). This variability is an outcome of different forestry management and the wide variety of environmental characteristics among the managed pine stands, such as elevation, slope, bedrock, soil and fire history (Schiller et al. 1997; Ne'eman and Izhaki 1999).

Although Israeli forests were originally planted for timber or fuelwood, they have never been used for these purposes. These forests suffered from diseases and over density and since the 80's the JNF (Jewish National Fund) forests are not used anymore for wood supply but treated to strengthen their diversity, sustainability and to improve their cultural services (Osem et al. 2014; Boneh 2015). The current policy aims are to create mixed, multi-layered with high biodiversity forests as well as forests with higher tolerance and better resilience to climate-change impacts (Boneh 2015). Thus, more and more natural vegetation (shrubs, trees and climbers) have appeared as the forests have aged (Oberhauser 1997). The consequence was that these forests have become more diverse by natural processes and have eventually become seminatural forests (Brockerhoff et al. 2008).

### Forest management to enhance biodiversity and ecosystem services

There is no doubt that biodiversity conservation is essential to maintain ecosystem services, given the

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complex ecological interactions between biotic and abiotic components that eventually benefit humans (Mace et al. 2012). Thus, forest biodiversity is important to support human existence and well-being (Osem et al. 2014). Indeed, the first priority of forest management policy in Israel nowadays is to offer recreational and outdoor activity (Osem et al. 2014; Storch et al. 2018). However, forest ecosystems worldwide provide many additional services, including conservation, supply of wood, improving soil quality (Fox 2000) and air quality (through air filtration), rainwater drainage (Bolund and Hunhammar 1999), climate regulation, carbon storage and natural pest control (for example, by providing night shelter for insectivorous birds) (Nasi et al. 2002).

The current approach of nature conservation authorities is that conservation efforts should not be limited to nature reserves and, therefore, should also be directed toward managed, seminatural forest areas (Harris 1984; Wilcove 1989; Hansen et al. 1991). In light of the conservation and ecological importance to maintain high biodiversity in managed forests, priority should be given to enrich the forest structure. There is a strong correlation between diversity composition and forest structure (Urban and Smith 1989). Thus, complexity in forest structure promotes wild plant and animal diversity (Hansen et al. 1991).

### Birds as bioindicators

A forest management policy that will encourage biodiversity should be based on research that clarifies whether different types of managed forests maintain different levels of biodiversity as well as how ecological attributes of different forest types affect biodiversity. Such knowledge will provide forest managers with recommendations on how to administer forests to support high biodiversity. However, it seems almost impossible to separate the effects of various management methodologies on biodiversity (Lindenmayer et al. 2000).

Many studies in various ecosystems have shown that birds can serve as bioindicators (Koskimies 1989; Daily et al. 1993; Canterbury et al. 2000; Mikusinski et al. 2001; Gregory et al. 2003; Gregory 2006; Padoa-Schioppa et al. 2006). It has also been documented that bird biodiversity can be enhanced by forest design and management (Fuller et al. 2007; Quine et al. 2007). In the Mediterranean region, forest birds are considered good bioindicators and also play important roles in ecosystem functioning (Gil-Tena et al. 2007). Furthermore, many bird species can be considered keystone species due to their important roles in ecosystems as predators, prey and pollinators (Daily et al. 1993). Bird density and diversity indicate the quality of the habitat for other organisms (Gregory et al. 2003), and thus bird-count data is relevant to land-management and conservation

decisions (Bock and Jones 2004). Bird censuses are efficient and indicate bird abundance and reproductive success over large spatial scales (Carignan and Villard 2002; Padoa-Schioppa et al. 2006).

In Israel, 30–41 bird species were observed in pine forests, including 65% all-year residents, 14% winter residents, 9% summer residents and 12% migratory birds (Izhaki and Adar 1997; Sorek and Pervolotsky 2016). Only 28% of these species are forest obligators whereas the other species inhabit the maquis (scrubland vegetation of the Mediterranean region) as well (Sorek and Pervolotsky 2016). However, field experiments designed to assess the impact of forest management on bird abundance and biodiversity are rare in Israel. In light of the fact that 7% of the lands in Israel are managed forests, it is rather surprising that the study of bird communities in Israeli forests has largely been overlooked (especially in central and northern Israel) (but see Rankevich and Warburg 1983; Izhaki and Adar 1997; Shochat et al. 2001).

The relationship between bird diversity and the environmental attributes of managed coniferous forests was, and still is, the subject of many studies in Europe (Patterson et al. 1995; Paillet et al. 2010; Rosenvald et al. 2011; Czeszczewik et al. 2015). Forest structure is an important factor in birds' habitat choice (Sweeney et al. 2011). The composition of bird communities is governed by the stage of forest growth and the understory characteristics that affect the aural, visual and physical environments (Schieck 1997; Whelan and Maina 2005). There are several factors that may increase species richness of forest birds: plantation size (Robbins 1980; Izhaki 2000), forest age (Izhaki 2000; Moning and Müller 2009), plant species richness (Lynch and Whigham 1984; Izhaki 2000), successional stage, understory composition (Izhaki 2000) and canopy height (Robbins 1980). As forests become denser with taller growing shrubs, trees and climbers, they support higher bird densities (Patterson et al. 1995; Sweeney et al. 2011) and biodiversity (Fuller 2003).

The main goal of our study was to establish recommendations for pine forest management policy in Israel. To that end, we have addressed the following specific questions: (1) How does forest structure influence bird community composition, richness abundance and complexity? (2) What is the effect of understory vegetation on bird diversity? The results and recommendations of this study could be applied in semi-arid forests across the Mediterranean basin.

## Methods

### Study plots

The study was carried out in a non-industrial, managed coniferous forests in northern Israel, from the Carmel

ridge in the west to Megido in the east. The climate of the area is typical for the Mediterranean with an annual rainfall of 600 to 700 mm, mainly concentrated between December and February (Goldreich 1994). Our bird survey included 20 forest plots, that were at least 250 m apart (Fig. 1) to minimize the potential for individual birds to be counted at multiple points (Shriner 2001; Brown et al. 2015). All plots were more than 50 years old and larger than 5 ha (JNF forest database 2015).

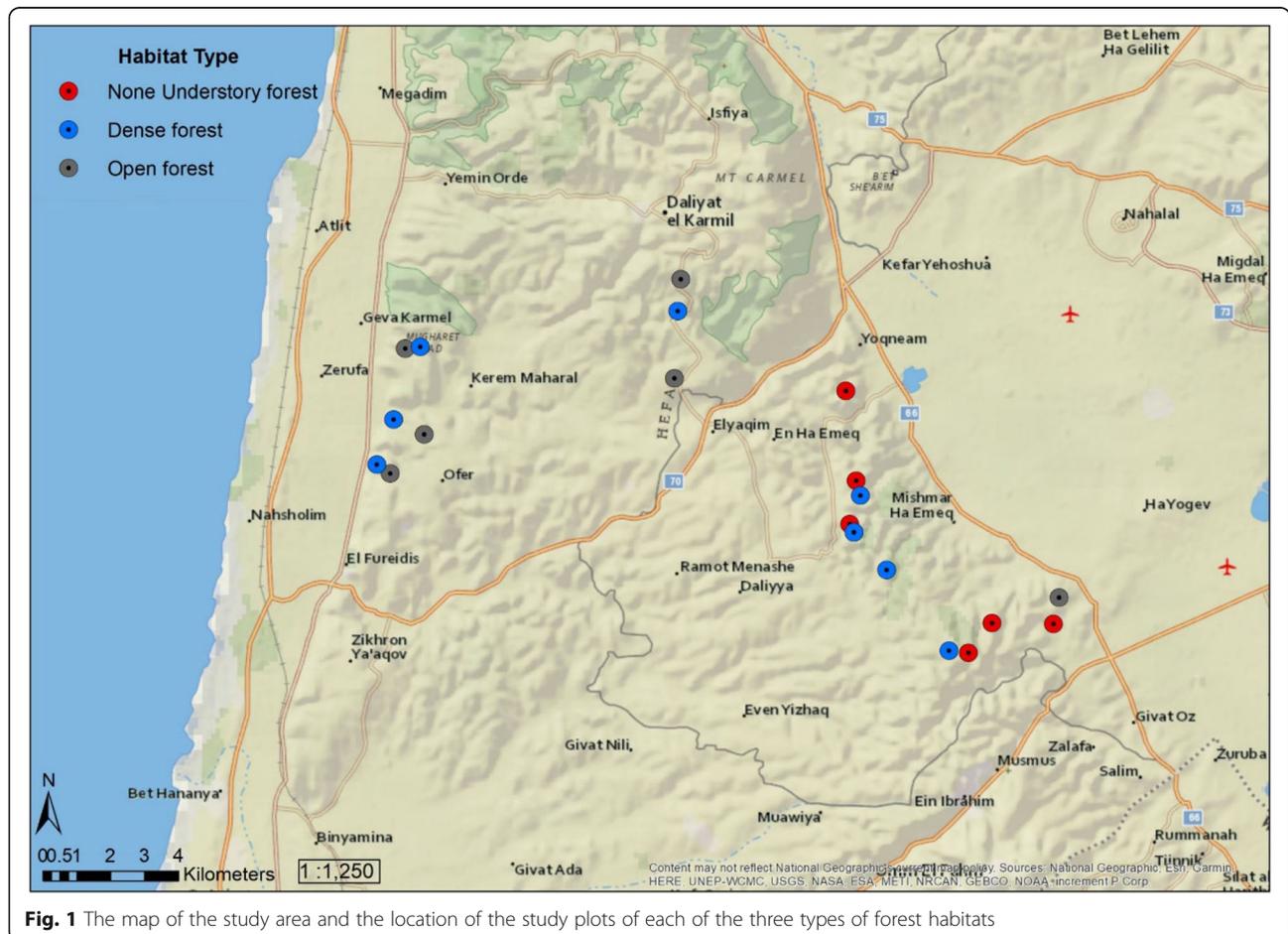
These forests were dominated by two planted pine species: Aleppo pine (*Pinus halepensis*) and Brutia pine (*Pinus brutia*). Tree density ranged from 1500 trees per ha with a limited number or an absence of shrubs, to an open forest with less than 500 trees per ha with shrubby patches and gaps with mainly herbaceous vegetation (Ne’eman and Izhaki 1999). The understory beneath the managed pine trees varied greatly among the study plots and constituted a mosaic of small trees such as *Quercus calliprinos* and *Pistacia palaestina*, shrubs like *Pistacia lentiscus*, *Phillyrea latifolia*, *Calicotome villosa*, *Rhamnus lycioides*, and climbers such as *Smilax aspera* and *Clematis cirrhosa* (Schiller et al. 1997). Habitat structure

in this study followed the definition of Smith et al. (2017) and included soil cover, tree density, tree height, tree volume, vegetation cover and more (for specific species and total coverage see Table 3 in Appendix).

We selected the study plots in the three main forest habitat types in our landscape (Fig. 1): (1) dense pine forest with a diverse understory of shrubs and shrub-like trees (DF,  $n = 8$  plots); (2) open pine forest with natural broadleaf trees and an understory of large shrubs (OF,  $n = 6$  plots); and (3) dense pine forest with (almost) no understory except herbaceous vegetation (NF,  $n = 6$  plots).

**Bird surveys**

Bird surveys were conducted at 20 fixed point counts (Bibby 2000), one point per study plot. The minimum distance between two points was 250 m, which is much above the recommended minimum distance between point-count stations (Huff et al. 2000). Each point count was located at least 50 m deep in the forest to avoid edge effect. A circular point-count method with a 50-m radius (Reynolds et al. 1980; Shriner 2001; Brown et al. 2015)



**Fig. 1** The map of the study area and the location of the study plots of each of the three types of forest habitats

was used to estimate bird density, species richness and diversity in each study plot (Sweeney et al. 2011; Brown et al. 2015). All birds heard or seen from the census station over a 10-min interval (Reynolds et al. 1980; Shriner 2001) were registered by species, date of detection and distance in 2 radius bands: 0 to 30 m and 30 m to infinity (plot edge) from the observer (Bibby 2000). Birds that were flushed from the plot when approaching the point count station were recorded as present in the counting time (Reynolds et al. 1980; Marsden 1998). Birds crossing in flight over the station (up to 25 m) during the census were counted (Reynaud and Thioulouse 2000).

Each point count was visited monthly in the fall (mid-August to late October), winter (late October to March), spring (March to June) and summer (June to mid-August) over two years (2015–2017). Thus, we visited each point count 24 times during this study. Bird counts were carried out in fine weather between sunrise and none in the spring, summer and fall, and between 07:00 and 14:00 in the winter. Point-count data was used to determine bird abundance, density (Patterson et al. 1995; Bibby 2000; Alldredge et al. 2007), richness (Patterson et al. 1995), diversity and community composition (Alldredge et al. 2007) in the three types of forest habitat.

#### Comparing habitat structure in the three types of forest habitat

The parameters of habitat structure (mainly vegetation measurements) were carried out by two transects at a 25-m radius around each point count and included the cover percentages of understory perennial species, herbaceous vegetation and exposed soil and rock surfaces (Schiller et al. 1997; Marsden 1998). Plant species were recorded every 10 cm along the transects and were categorized into life form, height level (Schiller et al. 1997) and species. The cover percentage of each species and life form was categorized into four layers: ground (below 1 m), shrub level (1 to 5 m), low canopy (5 m up to canopy level) and tree top level (Marsden 1998; Fuller 2003). The percentages were calculated independently for each life form, and therefore, the total cover percentage could reach more than 100% (Schiller et al. 1997; Ellis and Betts 2011). The following parameters were measured for pine trees: average percentage canopy cover, tree top height, tree diameter at breast height and tree density (Schiller et al. 1997; Czeszczewik et al. 2015). The vegetation survey was carried-out in spring 2017 in all plots.

#### Data analysis

Discriminate analysis was used to determine if the three types of forest habitat were indeed different in vegetation structure using SPSS21 (SPSS 2015). Non-metric

multidimensional scaling (NMDS) ordination was used to estimate the effect of vegetation characteristics (canopy cover percentage, understory cover percentage, trees per ha, etc.) on bird community composition in the three types of forest habitat. For this analysis we used R package *vegan* (Oksanen et al. 2016) and the *ade4* package (Dray and Dufour 2007), as well as the Monte Carlo method to test the significance of the results.

We used species network analysis to compare the complexity of the bird communities among the three forest types. To this end, we calculated three network parameters for each forest type for each season using the *igraph* R package (Csardi 2006): (a) normalized degree centrality which indicates the number of nearest neighbors of each bird species (nodes) divided by maximum possible degree, (b) weighted degree which indicates the sum of the frequency of interspecific associations and (c) closeness centrality which representing the distance between the species in the network.

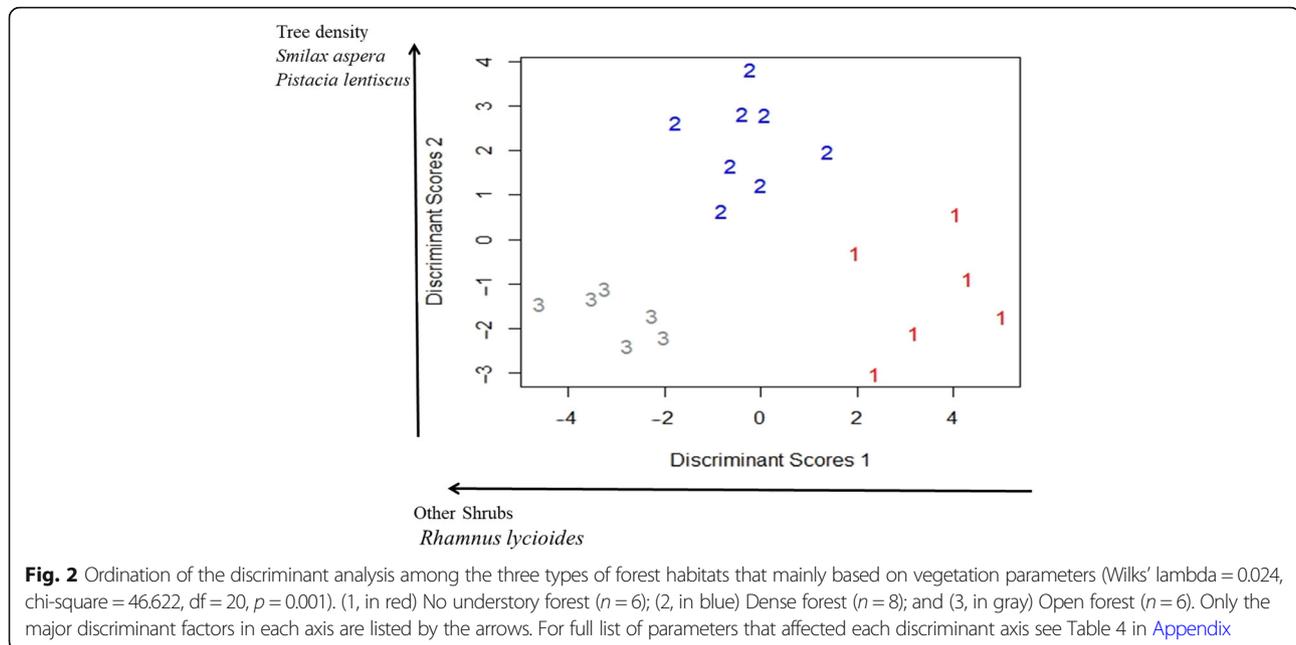
Bird species diversity and accumulation in each type of forest habitat were estimated by Chao1 a non-parametric index of predicted species richness, using in R package *vegan*. Bird abundance and density were calculated with R package *Distance* in (Miller 2016), within 30 m of the point count station and more than 30 m to the plot edge, using model that consider and calculate the change in detectability with distance and calculate the density per square m (Buckland et al. 2008).

We used ANOVA through R package *Stats* (R Core Team 2016) to compared the three different types of forest habitats for (a) parameters that were not included in the ordination - bird density, species richness and diversity per point count and (b) the three complexity indices in each season. ANOVAs were followed by Bonferroni multiple Comparison Tests. *p* values of less than 0.05 were considered significant for all tests.

## Results

### The structural difference among the three types of forest habitats

Linear Discriminant Analysis significantly showed that the three types of forest habitat were distinctive mainly based on vegetation attributes (Fig. 2, Table 4 in Appendix). The coverage of *Rhamnus lycioides* and other shrubs were the two predominant vegetation factors which affected the X-axis of the discrimination, whereas tree density and the coverage of *Smilax aspera* and *Pistacia lentiscus* were the main factors that contributed to the discrimination on the Y-axis (Fig. 2, Table 4 in Appendix). Thus, the main shrubs in the dense forest (DF) were *S. aspera* and *P. lentiscus* whereas the main shrub species in the open forest (OF) was *Rhamnus lycioides* (Fig. 2). *Rhamnus lycioides* in the OF had the highest coverage of  $61.9\% \pm 2.15\%$ , ( $n = 6$ ) representing both



horizontal and vertical vegetation coverage, but only  $25.4 \pm 1.1\%$ , ( $n = 8$ ) in the DF and  $2.2 \pm 1.93\%$ , ( $n = 6$ ) in the no understory (NF) plots. The tree density was the highest in the DF habitat ( $1525 \pm 363$  per ha,  $n = 6$ ), than in the NF habitat ( $1100 \pm 412$  per ha,  $n = 8$ ), and the low tree density was in the OF habitat ( $367 \pm 137$  per ha,  $n = 6$ ). Shrub coverage in the DF habitat was  $119\% \pm 28\%$  ( $n = 8$ ) and  $111\% \pm 13\%$  ( $n = 6$ ) in the OF habitat, whereas, in the NF habitat, only  $0.7\% \pm 0.81\%$  ( $n = 6$ ) of shrub coverage was found (Table 3 in [Appendix](#)). For the full list of habitat characteristics that affected the discriminant analysis between the three forest types see Table 3 in [Appendix](#).

#### The impact of habitat structure on bird community composition

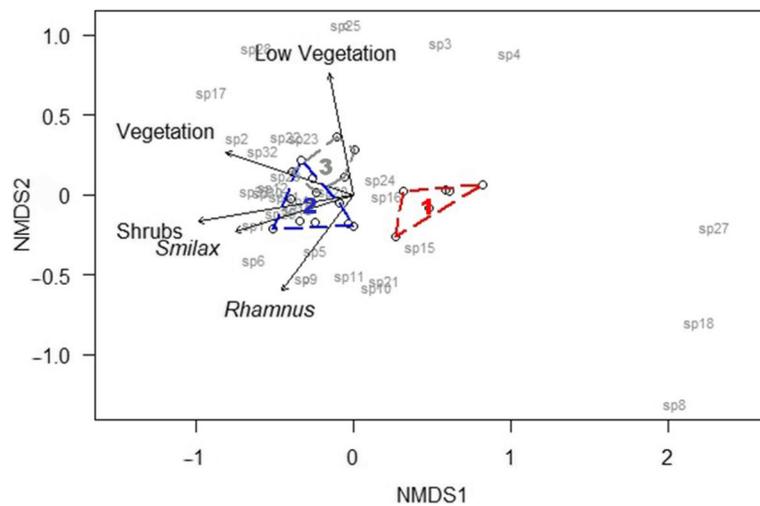
During this study, a total of 1476 birds of 33 species were observed over 189 survey days between 2015 and 2017. The full list of birds that were observed in each forest type appears in Table 5 in [Appendix](#). The NMDS ordination, which was based on all observations from all seasons, demonstrated that habitat structure, mainly the vegetation attributes was significantly associated (Monte Carlo test,  $p = 0.01$ ) with bird community composition (Fig. 3, Table 6 in [Appendix](#)). The bird communities in the two forest habitats with understory vegetation (DF and OF) were overlapped to some extent, whereas both were markedly different from the NF habitat (Fig. 2). The NMDS ordination plot shows that the composition of bird community was primarily affected by total shrub coverage ( $p = 0.001$ ), total vegetation cover ( $p = 0.024$ ),

*Rhamnus lycioides* coverage ( $p = 0.028$ ), *Smilax aspera* coverage ( $p = 0.047$ ) and low vegetation coverage ( $p = 0.043$ ), (Fig. 3, Table 6 in [Appendix](#)).

#### Bird abundance, richness and diversity in the three types of forest habitat

The most common bird species observed in this study (across the three types of habitat) were the Sardinian warbler (*Sylvia melanocephala*) with 459 individuals, the Common chaffinch (*Fringilla coelebs*) with 173 individuals and the Blackbird (*Turdus merula*) with 130 individuals. The bird community networks differed across the three forest types (Fig. 4). Three resident species (*S. melanocephala*, *Garrulus glandarius* and *Streptopelia decaocto*) consistently presented across the three forest types (see also Table 5 in [Appendix](#)). Compared to their relatively high abundance in the DF and OF habitats, the European robin (*Erithacus rubecula*) was not spotted in the dense pine forest with no understory (NF). Two species (Great tit, *Parus major*, and Blackbird, *Turdus merula*) were also very rare in the (NF) habitat (Table 1). On the other hand, the abundance of Common chaffinch (*Phylloscopus collybita*) was higher in the NF habitat, but not significantly (Table 1).

The network complexity was far greater in the open and dense habitats (OF and DF, respectively) in comparison with the forest without understory (NF) in each season (Fig. 5). The species in the NF forest significantly associated with a proportionately lower number of other species (normalized degree) in fall and winter but not in spring (Fig. 5a) and a lower frequency of interspecific

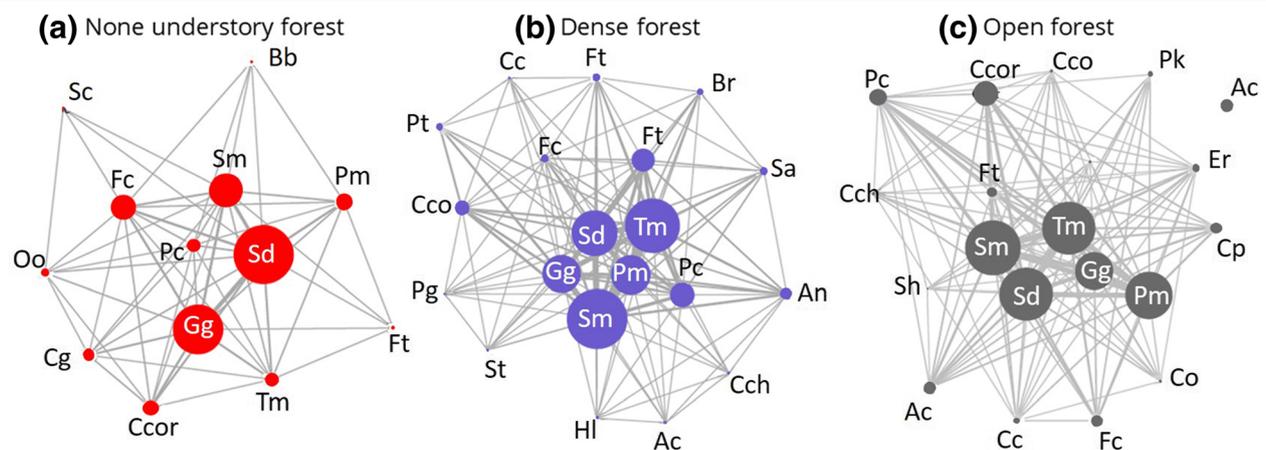


**Fig. 3** NMDS ordination of the bird species in relation to the habitat structure parameters in three types of forest habitats: No understory forest, NF (1), Dense forest, DF (2) and Open forest, OF (3). Significant separation between the No understory forest habitat and the other two habitats are marked in polygons (NF in red, DF in blue, OF in gray). Bird species are marked in light grey numbers (for full bird names see Table 5 in [Appendix](#)); plots are marked by circles and arrows represent vectors of the significant factors that contributed to the ordination ( $p < 0.05$ ); See Table 6 in [Appendix](#) for more information on the statistical results of the MNDS ordination

associations (weighted degree) than did species in the other two forest habitats, however, it was significant only in fall (Fig. 5b). The distance among species (closeness) was significantly larger in the NF forest than the other two forest types in spring but with no significant differences in the other two seasons (Fig. 5c).

Total bird density was significantly higher in the two types of forests with developed understory vegetation in

comparison with the forest without understory vegetation (One-way ANOVA,  $F = 27.32$ ,  $df = 2, 17$ ,  $p < 0.001$ , Fig. 6). The differences among the three types of forest habitats remained when bird density was analyzed by season (Fig. 7, Table 7 in [Appendix](#)). In spring, the difference in bird density between the three types of forest habitats narrowed and was not significant. In the summer, bird density in the DF habitat was similar to both NF and OF habitats.



**Fig. 4** Example of bird community networks (Spring only) in three pine forest types in northern Israel: Dense forest (DF) and Open forest (OF) both with developed understory vegetation and a pine forest without understory (NF). Species are represented by the circles (nodes) and interactions are represented by the links. Node sizes are proportional to total number of observations of each bird species. An, *Accipiter nisus*; Ac, *Alectoris chukar*; Bb, *Buteo buteo*; Cc, *Carduelis carduelis*; Cch, *Carduelis chloris*; Cg, *Clamator glandarius*; Cco, *Coccothraustes coccothraustes*; Ccor, *Corvus cornix*; Co, *Cinnyris osea*; Cp, *Columba palumbus*; Er, *Erithacus rubecula*; Fc, *Fringilla coelebs*; Ft, *Falco tinnunculus*; Gg, *Garrulus glandarius*; Hl, *Hippolais languida*; Oo, *Oriolus oriolus*; Pc, *Phylloscopus collybita*; Pg, *Prinia gracilis*; Pk, *Psittacula krameri*; Pm, *Parus major*; Pt, *Phylloscopus trochilus*; Sa, *Sylvia atricapilla*; Sd, *Streptopelia decaocto*; Sh, *Sylvia hortensis*; Sm, *Sylvia melanocephala*; St, *Streptopelia turtur*; Tm, *Turdus merula*; Tt, *Troglodytes troglodytes*

**Table 1** The total numbers of the most common 10 bird species observed in the three types of forest habitats (normalized by number of visits per site, all seasons pooled)

Species name	Common name	No understory forest	Dense forest	Open forest	Total
<i>Sylvia melanocephala</i>	Sardinian warbler	17 <sup>a</sup>	185 <sup>b</sup>	196 <sup>b</sup>	459**
<i>Fringilla coelebs</i>	Common chaffinch	61	40	59	173
<i>Turdus merula</i>	Blackbird	4 <sup>a</sup>	52 <sup>b</sup>	57 <sup>b</sup>	130**
<i>Phylloscopus collybita</i>	Chiffchaff	21	43.5	48	127
<i>Streptopelia decaocto</i>	Collared dove	31	28	47	115
<i>Parus major</i>	Great tit	7 <sup>a</sup>	37 <sup>b</sup>	58 <sup>b</sup>	114*
<i>Garrulus glandarius</i>	Eurasian jay	29	32	28	99
<i>Erithacus rubecula</i>	European robin	0 <sup>a</sup>	22 <sup>b</sup>	34 <sup>b</sup>	65*
<i>Columba palumbus</i>	Common wood pigeon	13	0	43	56
<i>Corvus cornix</i>	Hooded crow	4	13	12	33

(\*) significantly lower abundance, a  $p$ -value of  $p < 0.001$ , in one-way ANOVA (different letters above bars indicate significant differences, Bonferroni Multiple Comparison Test,  $p < 0.05$ )

(\*\*) significantly lower abundance, a  $p$ -value of  $p < 0.0006$ , in one-way ANOVA (different letters above bars indicate significant differences, Bonferroni Multiple Comparison Test,  $p < 0.05$ )

However, in winter and fall both DF and OF habitats were significantly more dense in birds than the NF habitat (Fig. 7).

There were also significant differences in bird richness and diversity among the three types of habitat. Whereas the NF habitat was significantly lower in all indices of richness and diversity than the DF and OF habitats (Table 5 in Appendix), there was no significant difference in any index of richness and diversity between the DF and OF habitats (Table 2). The expected species accumulation curves (Fig. 8) in the three types of forest habitats were not reached a plateau; thus, more species are expected to be found with more bird surveys. The NF habitat had a significantly ( $F = 510.2$ ,  $df = 2, 147$ ,  $p < 0.001$ ) lower species richness curve and the OF habitat had the highest curve. The expected richness of all three types of habitat together were higher than the curves of expected richness of each of the two DF and OF habitats. Furthermore, landscape gamma diversity of the three types of forests (33 bird species) was much higher than alpha diversity of each type of forest alone (Table 5 in Appendix).

## Discussion

### The structural difference among the three types of forest habitat

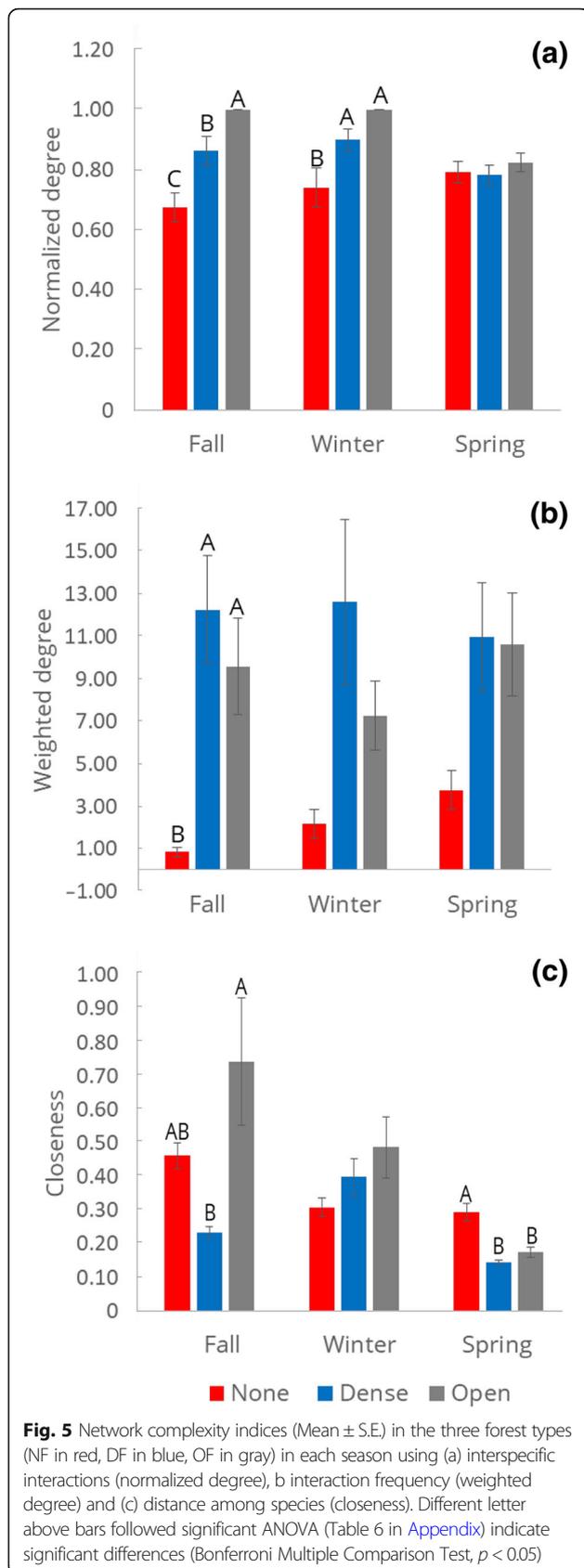
The three types of habitat that were studied can be categorized into two groups: one of the forest habitats had no understory (NF) whereas two of them (OF and DF) had a developed understory vegetation with > 100% vegetation cover. However, the OF and DF habitats were significantly different in their understory composition and pine density. It should be emphasized that since all of these forests were planted 50 to 56 years

ago, there was no planned management that aimed to create various types of forest. The JNF current policy is to maintain sustainable management of forests that support high biodiversity and offer recreational and outdoor activity (Osem et al. 2014). Furthermore, the forests nowadays are barely treated (e.g., thinning, cutting, grazing) in recent decades. Thus, the development of the different types of forest habitats that we see today is mainly due to natural processes and fires rather than human planning.

The outcome is that these forests create a mosaic of heterogeneous habitats with high structural diversity of vegetation (Schall et al. 2018; Schulze et al. 2019). Consequently the heterogeneity among these three types of habitat will contribute to great richness and diversity across the whole landscape (Freemark and Merriam 1986; Brotons et al. 2005). Furthermore, a wide variety of vegetation is associated with the diversity of various fauna groups (Paillet et al. 2010; Irwin et al. 2014). Indeed, our study suggests that the combination of the three types of forest habitat also contributes to the overall richness and diversity of the bird community across the planted pine forests, as a mosaic-type forest landscape (Izhaki 2000).

### The impact of vegetation attributes on bird community structure

It has been previously documented that birds are affected by the structure of forest vegetation (Huang et al. 2014; Ferger et al. 2014; Vogeler et al. 2014). The study plots of the three types of habitat were close to each other (the maximum distance between two study plots was 20 km), located at the same altitude and in the same climatic zone, and had similar primary forest



plantations of the same age. Nonetheless, the results clearly demonstrate that at least two types of habitat (OF and DF) had a unique bird community and diversity in comparison to the third one (NF).

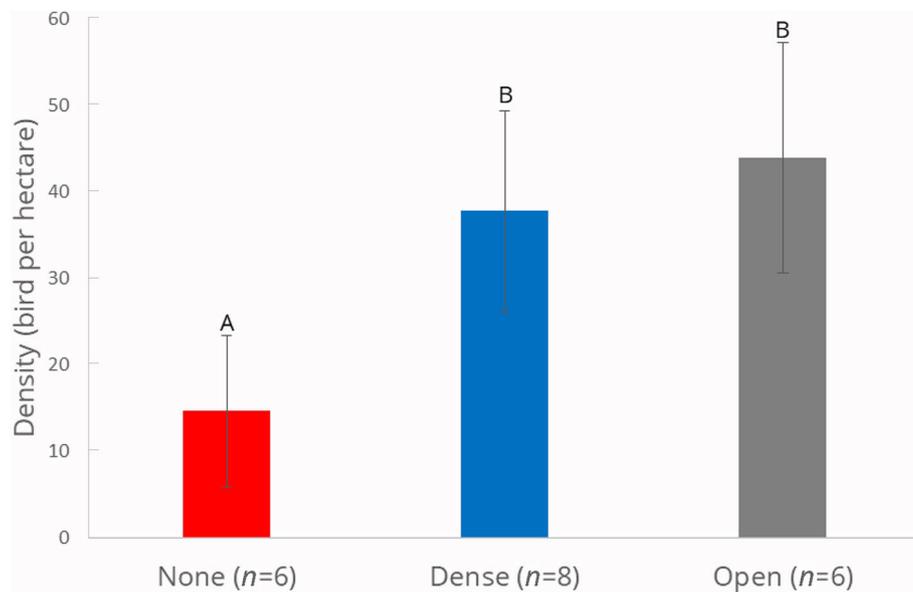
The main structural component of vegetation that had the highest influence on bird presence in this study was shrubs. *Rhamnus lycioides*, a very common Mediterranean spiny shrub, is one of the few woody shrub species that can establish itself in pine plantations (Moreno-Gutiérrez et al. 2015). *Rhamnus lycioides*, *Pistacia lentiscus*, *Smilax aspera* and *Asparagus aphyllus* are all produce edible fruits (during the fall and winter) and thus attracts frugivorous species, such as the Sardinian warbler and the Eurasian blackcap (*Sylvia atricapilla*) (Izhaki 2000). Gil-Tena et al. (2007) and Sweeney et al. (2010) reported similar results, demonstrating the importance of shrubs in the forest for bird refuge, foraging and breeding.

The understory is the key factor for the presence and abundance of several bird species. Great tit (*Parus major*) was significantly selective in our study, requiring a well-developed understory shrub layer. Similar results were reported by Díaz (2006) in Spanish woodlands and forests, where Great tit preferred mature pinewoods with developed understory vegetation. Similarly, in our study Blackbirds (*Turdus merula*) were totally absent from the NF habitat and preferred a highly developed understory shrub layer. This preference was also observed in the Western Mediterranean area of Spain (Díaz 2006) and in Switzerland (Von Dem et al. 2008).

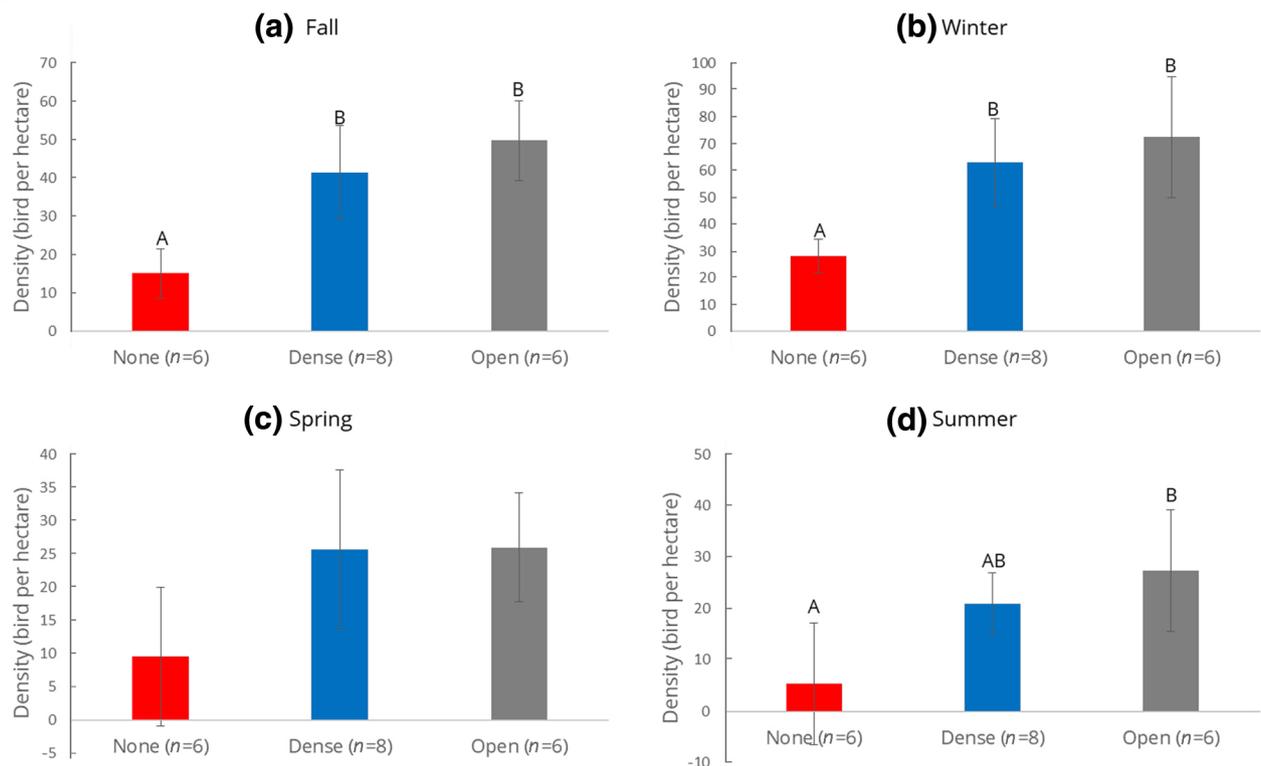
The European robin (*Erithacus rubecula*) was also completely absent from the NF habitat in our study and preferred the OF habitat, which is practically a shrubland with sparse trees. Tellería and Perez-Tris (2004) showed a contrasting phenomenon, where this species preferred forests over shrubland, considering the forest as a nesting site and therefore as a strong territorial site. Our study showed that the understory creates a powerful microhabitat that attracts the European robin, and without this understory layer this forest would be rather empty of robins.

#### Bird community complexity, richness, diversity and abundance in the three types of forest habitat

The three types of forest habitat are significantly different in terms of network complexity, bird abundance, richness and diversity. The positive effect of vegetation heterogeneity on forest and woodland bird species richness is well established in studies across the world (Koh et al. 2006; Davies et al. 2007; Huang et al. 2014). The NF habitat in this study lacks understory vegetation and therefore represents a homogenous rather than heterogeneous forest. Consequently, the NF habitat maintains lower bird species richness as well as much lower community complexity, as in monoculture forests (Erskine et al. 2006). The difference



**Fig. 6** Total bird density per ha (mean  $\pm$  SE) in the three forest habitats. Higher bird density was found in the Dense forest (DF in blue) and Open forest (OF in gray) habitats in comparison with the No understory (NF in red) habitat (different letters above bars indicate significant differences, Bonferroni Multiple Comparison Test,  $p < 0.05$ )



**Fig. 7** Bird density per ha (mean  $\pm$  SE) in the three types of forest habitat, per season higher bird density was found in the Dense forest (blue) and Open forest (gray) habitats in comparison with the No understory (red) forest habitat (different letters above bars indicate significant differences (Bonferroni Multiple Comparison Test,  $p < 0.05$ )

**Table 2** Bird diversity and abundance scores in the three types of forest habitat (all seasons pooled)

	Average abundance (per visit)	Density (birds per ha)	Chao index	Expected richness	Total number of individuals	Visits
NF	4.2 <sup>a</sup>	15.4 <sup>a</sup>	11.2 <sup>a</sup>	15.7 <sup>a</sup>	197 <sup>a</sup>	52
DF	11.6 <sup>b</sup>	38.2 <sup>b</sup>	16.9 <sup>b</sup>	20.5 <sup>b</sup>	658 <sup>b</sup>	72
OF	13.7 <sup>b</sup>	43.8 <sup>b</sup>	16.8 <sup>b</sup>	22.0 <sup>b</sup>	613 <sup>b</sup>	56
<b>F</b>	21.7	4	10.7	10.2	8.5	
df (degrees of freedom)	2	2	2	2	2	
<b>p*</b>	< 0.001	< 0.03	< 0.001	< 0.001	< 0.001	

\*One-way ANOVA (different letters above bars indicate significant differences, Bonferroni Multiple Comparison Test,  $p < 0.05$ )

between a monoculture forest and a monoculture forest with well-developed understory vegetation was also a key factor affecting species richness in other studies (Lugo 1997; Azor et al. 2015). Likewise, in the OF and DF habitats, where the understory vegetation is well developed, we found more bird species and higher diversity.

The age of the pine forest can be a contributing factor to bird species richness through the development of the understory layer over time (Hobson and Bayne 2000; Díaz 2006; Gil-Tena et al. 2007). However, in the current study, although the plantation time of all forest plots was similar, a marked difference in the growth of the understory vegetation was observed among the three types of habitat. Therefore, we were able to examine the impact of understory vegetation on bird species richness while controlling for forest age.

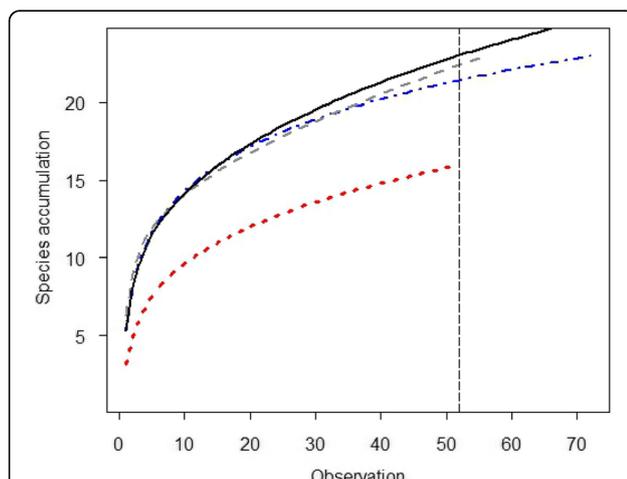
Plots with developed understory vegetation plots showed significantly high diversity, similar to the results of other studies (Izhaki 2000; Nilsson and Wardle 2005).

The growth of shrubs and young trees seems to appeal to birds in our study area. The wild, dense evergreen woodland in the Mediterranean basin is based primarily on low trees and shrubs (Perevolotsky and Haimov 1992). Therefore, most of the birds observed in this study were typical to wild shrublands and dense woodlands. For example, the Sardinian warbler (Bas et al. 2005), which normally avoids pine plantations (Rey-Benayas et al. 2010), was observed numerous times in this study in the pine forests, mostly in forest plots with rich understory.

## Conclusions

Indeed, managed forest in sustainable matter can provide both wood for human uses rich biodiversity (Liang et al. 2016). But, since the industrial forestry in Israel was not successful, it is unfortunate that some of the ecological services from pine forest are not provided, and moreover, import from wood from other forests is forced.

A shrub layer provides food diversity, refuge and breeding sites by increasing the heterogeneity of the forest habitat (Izhaki 2000; Bonham et al. 2002; Díaz 2006; Sweeney et al. 2010). Vegetation cover under the canopy of the forest is key to the increase in species diversity and richness (Kirk and Hobson 2001; Ross et al. 2001; Herrando and Brotons 2002; Golet et al. 2001). The past management of industry forests dramatically reduced the understory and produced an almost “green desert” forest (Dyer et al. 2004). We suggest that the natural succession in planted pine forests, such as seed dispersal by birds, should be encouraged, as long as no timber production is expected in the future from these pine trees. We also recommend that forest managers actively promote understory vegetation by thinning the pine forest and allowing understory vegetation to establish. Such a management policy will create heterogeneous seminatural forests that maintain high biodiversity, instead of the originally planned monoculture of pine forests for the industry.



**Fig. 8** Species accumulation curves estimated by Chao1 of the No understory forest habitat (red dots), the Dense forest habitat (blue dash-line) and the Open forest habitat (gray dash). Letters represent Bonferroni test ( $p < 0.05$ ). The No understory forest habitat is significantly different in species accumulation from the Dense forest and Open forest habitat. The black curve represents all three types of forest habitat combined. The vertical line represents the lowest number of observations per site

**Appendix**

**Table 3** Parameters used to characterize the habitat structure of each of three types of forest habitats

Parameter	No understory forest (n = 6)		Dense forest (n = 8)		Open forest (n = 6)	
	Average	SD	Average	SD	Average	SD
Soil (cover percentage)	12.09%	11.47%	13.86%	9.09%	15.37%	14.54%
Low trees (cover percentage)	0	0	65.11%	98.14%	35.28%	45.97%
Shrubs (cover percentage)	0.73%	1.64%	119.49%	56.23%	111.92%	26.77%
Total vegetation (cover percentage)	12.83%	11.72%	198.46%	128.29%	162.57%	52.75%
Trees per ha	1100.00	412.31	1525.00	263.39	366.67	137.44
Average tree height (m)	18.57	1.91	17.25	2.34	16.66	2.02
Average tree volume (cm)	96.93	12.31	91.82	7.42	103.37	0.28%
<i>Smilax aspera</i> (cover percentage)	2.78%	4.47%	58.03%	34.61%	24.79%	39.17%
<i>Asparagus aphyllus</i> (cover percentage)	5.75%	12.75%	29.95%	34.93%	2.53%	2.10%
<i>Pistacia lentiscus</i> (cover percentage)	0.24%	0.54%	60.76%	48.29%	26.26%	28.50%
<i>Rhamnus lycioides</i> (cover percentage)	2.25%	3.88%	25.50%	22.16%	61.93%	43.06%

**Table 4** The correlation between the habitat structure parameters and the standardized canonical discriminant functions. Parameters ordered by absolute size of correlation within function

	Function	
	1	2
Other shrubs coverage	-0.431	0.354
<i>Rhamnus</i> coverage	-0.299	-0.101
Tree height	0.129	-0.026
Soil coverage	-0.039	-0.003
Trees per hectare	0.306	0.727
<i>Smilax</i> coverage	-0.125	0.345
<i>Pistacia</i> coverage	-0.130	0.331
<i>Asparagus</i> coverage	0	0.280
Tree volume	-0.067	-0.194
Low trees	-0.086	0.167

**Table 5** Total number and diversity indices (Alpha and Gamma) of birds observed in each type of forest habitat during the study (all seasons pooled)

Species name	Dense forest (DF)	No understory forest (NF)	Open forest (OF)	Total
<i>Accipiter nisus</i>	10	1	1	12
<i>Alectoris chukar</i>	10	0	9	19
<i>Aquila pomarina</i>	1	1	0	2
<i>Buteo buteo</i>	0	1	1	2
<i>Carduelis carduelis</i>	1	0	2	3
<i>Carduelis chloris</i>	4	0	4	8
<i>Cinnyris osea</i>	0	0	1	1
<i>Clamator glandarius</i>	0	3	0	3
<i>Coccothraustes coccothraustes</i>	0	0	1	1
<i>Columba palumbus</i>	0	13	43	56
<i>Corvus cornix</i>	17	4	12	33
<i>Erithacus rubecula</i>	31	0	34	65
<i>Falco subbuteo</i>	2	0	0	2
<i>Falco tinnunculus</i>	4	1	6	11
<i>Fringilla coelebs</i>	53	61	59	173
<i>Garrulus glandarius</i>	42	29	28	99
<i>Hippolais languida</i>	1	0	0	1
<i>Oriolus oriolus</i>	0	2	0	2
<i>Parus major</i>	49	7	58	114
<i>Phylloscopus collybita</i>	58	21	48	127
<i>Phylloscopus trochilus</i>	6	0	0	6
<i>Prinia gracilis</i>	1	0	0	1
<i>Psittacula krameri</i>	0	0	2	2
<i>Scolopax rusticola</i>	2	0	0	2
<i>Streptopelia decaocto</i>	37	31	47	115
<i>Streptopelia turtur</i>	1	0	0	1
<i>Sylvia atricapilla</i>	3	0	1	4
<i>Sylvia curruca</i>	0	1	0	1
<i>Sylvia hortensis</i>	0	0	1	1
<i>Sylvia melanocephala</i>	246	17	196	459
<i>Troglodytes troglodytes</i>	10	0	1	11
<i>Turdus merula</i>	69	4	57	130
<i>Turdus philomelos</i>	0	0	1	1
<b>Total</b>	<b>658</b>	<b>205</b>	<b>613</b>	<b>1476</b>
Alpha Diversity	<b>23</b>	<b>16</b>	<b>23</b>	
Gamma Diversity				<b>33</b>

**Table 6** The results of the MNDS ordination analysis of bird communities in relation to habitat structure (Fig. 3)

	NMDS1	NMDS2	$r^2$	$P$
Low vegetation cover	-0.2013	0.97953	0.3071	0.043
Low tree cover	-0.78272	0.62238	0.1066	0.319
Shrubs cover	-0.97886	-0.20451	0.5362	0.001
Total vegetation cover	-0.98254	0.18607	0.3777	0.024
Trees per ha	0.10147	0.99484	0.0434	0.701
Tree height	0.37536	0.92688	0.1854	0.18
Tree volume	-0.97843	0.20659	0.0032	0.972
Smilax aspera cover	-0.90532	-0.42473	0.3133	0.047
Pistacia lentiscus cover	-0.8954	0.44525	0.2221	0.107
Rhamnus lycioides cover	-0.56554	-0.82472	0.3504	0.028
Asparagus aphyllus cover	-0.63062	0.77609	0.1585	0.210

**Table 7** The effect of pine forest types in northern Israel (Dense forest, DF and Open forest, OF, both with developed understory vegetation and a pine forest without understory, NF) on the three complexity indices in each season using ANOVA

Season		Type III sum of squares	df	Mean square	$F$	Sig.
Normalized degree						
Fall	Corrected model	0.486 <sup>b</sup>	2	0.243	15.616	0.000
	Intercept	21.552	1	21.552	1383.898	0.000
	Habitat	0.486	2	0.243	15.616	0.000
	Error	0.436	28	0.016		
	Total	24.042	31			
	Corrected total	0.922	30			
Spring	Corrected model	0.018 <sup>c</sup>	2	0.009	0.471	0.627
	Intercept	32.062	1	32.062	1663.980	0.000
	Habitat	0.018	2	0.009	0.471	0.627
	Error	0.944	49	0.019		
	Total	34.268	52			
	Corrected total	0.962	51			
Winter	Corrected model	0.262 <sup>d</sup>	2	0.131	12.842	0.000
	Intercept	19.497	1	19.497	1910.898	0.000
	Habitat	0.262	2	0.131	12.842	0.000
	Error	0.245	24	0.010		
	Total	22.634	27			
	Corrected total	0.507	26			
Weighted degree						
Fall	Corrected model	649.161 <sup>b</sup>	2	324.581	6.349	0.005
	Intercept	1722.839	1	1722.839	33.700	0.000
	Habitat	649.161	2	324.581	6.349	0.005
	Error	1431.442	28	51.123		
	Total	4251.940	31			
	Corrected total	2080.603	30			
Spring	Corrected model	482.364 <sup>c</sup>	2	241.182	2.533	0.090
	Intercept	3587.223	1	3587.223	37.680	0.000

**Table 7** The effect of pine forest types in northern Israel (Dense forest, DF and Open forest, OF, both with developed understory vegetation and a pine forest without understory, NF) on the three complexity indices in each season using ANOVA (*Continued*)

Season		Type III sum of squares	df	Mean square	F	Sig.
Winter	Habitat	482.364	2	241.182	2.533	0.090
	Error	4664.930	49	95.203		
	Total	9404.414	52			
	Corrected total	5147.294	51			
	Corrected model	422.295 <sup>d</sup>	2	211.147	3.049	0.066
	Intercept	1364.453	1	1364.453	19.706	0.000
	Habitat	422.295	2	211.147	3.049	0.066
	Error	1661.778	24	69.241		
	Total	3867.003	27			
	Corrected total	2084.073	26			
Closeness						
Fall	Corrected model	1.477 <sup>b</sup>	2	0.739	5.068	0.013
	Intercept	6.915	1	6.915	47.442	0.000
	Habitat	1.477	2	0.739	5.068	0.013
	Error	4.081	28	0.146		
	Total	12.500	31			
	Corrected total	5.558	30			
Spring	Corrected model	0.184 <sup>c</sup>	2	0.092	21.695	0.000
	Intercept	2.106	1	2.106	497.332	0.000
	Habitat	0.184	2	0.092	21.695	0.000
	Error	0.207	49	0.004		
	Total	2.339	52			
	Corrected total	0.391	51			
Winter	Corrected model	0.127 <sup>d</sup>	2	0.063	1.267	0.300
	Intercept	3.995	1	3.995	80.016	0.000
	Habitat	0.127	2	0.063	1.267	0.300
	Error	1.198	24	0.050		
	Total	5.972	27			
	Corrected total	1.325	26			

**Abbreviations**

DF: Dense pine forest with a diverse understory of shrubs and shrub-like trees;  
 NF: Dense pine forest with (almost) no understory except herbaceous  
 vegetation; OF: Open pine forest with natural broadleaf trees and an understory  
 of large shrubs

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**Authors' contributions**

UD and II designed the study. UD collected all the data. UD and II analyzed the  
 data and wrote the manuscript together. Both authors read and approved the  
 final manuscript.

**Ethics approval and consent to participate**

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**Consent for publication**

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The authors declare that they have no competing interests.

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