The Importance of Annual Plants and Multi-Scalar Analysis for Understanding Coastal Dune Stabilization Process in the Mediterranean

Pua Bar Kutiel and Michael Dorman

Abstract: Since ecological phenomena and patterns vary with scale, scalar analysis is a developing practice in ecology. Scalar analysis is most valuable in heterogeneous environments, since habitat heterogeneity is a key factor in determining biodiversity. One such case can be seen in the changes in annual vegetation in coastal sand dune systems. Most studies in these environments are carried out at the dune scale, comparing dunes at different stabilization states. However, a broader understanding of dune stabilization processes requires analyses at the finer scales of dune slope aspects (directions of exposure to wind) and patches (under and between woody perennial species). Here, we present the results of a study that combines the three scales (dune, slope, and patch) in the Mediterranean coastal dune systems in Israel. Through this multi-scalar analysis, we are able to describe processes at the finer patch and aspect scale and explain how they shape patterns at the dune scale. The results indicate that the dune scale exposes the differences in annual plant characteristics between mobile and fixed dunes, their slopes and patches and the reorganization and spatial distribution of annual plants within mobile and fixed dunes during the stabilization process.

Keywords: annual plants; coastal dunes; fixed dunes; mobile dunes; dune stabilization; Mediterranean; open and shrub patches; slope aspects

1. Introduction

As a science that discusses spatial and temporal variations and dynamics, ecology is sensitive to differences in spatial and temporal scales [1]. Since some phenomena and mechanisms are observable only at certain scales, while others may exhibit contrasting patterns at various scales, scale is a fundamental theoretical and methodological issue (e.g., [2–6]). Wiens [2] has emphasized the importance of understanding processes at finer scales for understanding patterns at broader scales. McGill [7] has demonstrated how the abundance and distribution of species are determined by variables of different spatial scales, and thus how multi-scalar analysis is sometimes essential for understanding ecological phenomena. The issue of scale becomes more important when biodiversity and landscape ecology are discussed. Biodiversity is partly maintained by habitat heterogeneity [8], which is manifested in differences between habitats at different scales, from larger scales such as climatic gradients to smaller scales such as the immediate environment of a single organism.

Wheatley and Johnson [5] have distinguished between spatial and scalar analyses. Spatial analysis deals with the locations of entities and distances between them and is independent of sizes of observational units (grains). On the other hand, scalar analysis deals with changes in the observations at different grain sizes. We suggest that scalar analysis should be further subdivided into size and entity-defined scalar analyses. In a size-defined scalar analysis, grains are defined according to their sizes (e.g., 2 or 0.5 m scales), with less regard to the entities that construct landscape heterogeneity (i.e., what is inside the grain measurement unit). In an entity-defined scalar analysis, grains are defined first...
based on their identity and the entities inside them (e.g., the patch or community scales; see also [2,6,9]), and less by their sizes, so measurement units at different scales may be of the same size (i.e., nested structure of plots of the same size). Intermediate designs, in which equal or almost equal emphasis on both size and entity is given, may also exist.

Sand dunes are an environment in which multiple scales of habitat heterogeneity are very obvious (e.g., [10]). Wind drift potential and vegetation cover determine sand mobility [11], and thus the percentage of vegetation cover and the stabilization state of dunes are most commonly discussed as the key independent variables [11–20]. Dunes at different stabilization states also differ in terms of their vegetation composition. Mobile dunes usually support psammophilous species, while fixed dunes usually support non-psammophile species (such as generalist species) [12,13,21]. Since variation in dune stabilization states is currently a pressing issue [16,19–31], most studies have focused on the dune scale. Studies at the dune scale commonly describe differences among dune stabilization states and discuss the processes dunes undergo as they stabilize. Ecologically, these include an increase in species richness following the establishment of non-psammophile species, and usually the loss of psammophilous species [15,18,20].

Barchans and parabolic dunes are common types of dunes in regions where the common wind blows in one direction [32]. They are comprised of three slopes that differ in their abiotic conditions: the windward, that is exposed to wind erosion; the crest, with zero net sand erosion deposition but with greater exposure to wind; and the leeward slip face subjected to sand deposition [32]. The differences in wind activity and erosion-deposition balance among the three dune aspects affect plants’ ability to establish and survive. Thus, there are also apparent differences in geomorphic and ecological processes at the slope scale [14,23,28,33,34]. Consequently, plant species are not homogeneously distributed on dunes or among slopes; on fixed dunes, vegetation cover is distributed more homogeneously among slopes compared to mobile dunes [14,23,33–38].

Vegetation patches constitute a finer scale. Wind activity in mobile dunes constrains plant establishment, usually resulting in the formation of small vegetation patches (hereafter referred to as shrub patches) in an otherwise barren open matrix (open patches). The shrub patches themselves reduce wind drift potential and can facilitate the establishment of more vegetation, mainly on mobile and semi-fixed dunes [11,39,40]. The patchy distribution of vegetation is also maintained on the fixed dunes [35,41]. Studies at the patch scale usually focus on shrub patches, the effects of woody perennial plant species on their immediate surroundings and on vegetation (often annual plants) under shrub canopies [42–48]. The matrix in the open patches between perennial vegetation patches was once thought to be hardly affected by the woody perennial vegetation, but it is now evident that the effects of perennial plants can exceed the limits of their canopies and that the effects of shrubs on the vegetation differ between shrub and open patches [13,23,33,35,47,49].

Therefore, entity-defined multi-scalar analysis has the potential to reveal the complexity behind the general term “dune stabilization”, providing a broad perspective of the processes that dunes undergo during stabilization at different scales, elucidating the effects of the establishment of perennial species on their immediate environment (shrub patches) and surroundings (open patches) in different dune slope aspects and stabilization states. In this paper, we demonstrate the importance of studying vegetation at multiple entity-defined scales through analyses of the annual vegetation on coastal Mediterranean sand dunes. Our baseline for analysis is the commonly discussed dune scale. We then turn to the finer scales of the slope and patch types. We demonstrate that different information is acquired from analyses at each scale and show how the information contributes to the overall description of the annual vegetation at the study site, its variability, dynamics and possible governing processes.
2. Materials and Methods

2.1. Study Site

The study was conducted at the Nizzanim Long-Term Ecological Research (LTER) site in Nizzanim Dunes Nature Reserve, located at the southern part of the Mediterranean coastal plain, Israel (31°42′–31°44′ N, 34°35′–34°36′ E), covering an area of 20 km² (Figure 1). The site consists of mobile, semi-fixed and fixed dunes, separated by densely vegetated inter-dune depressions [16,18]. In the present study, we focused on the mobile (hereafter M) and fixed dunes (hereafter F)—the two extreme states. The climate is Mediterranean with an annual average temperature of 20 °C and annual rainfall of 400–500 mm falling mainly during winter (November–April). The common wind direction is south-west with a very low drift potential index (147) [38].

Figure 1. A map of Israel, indicating the location of Nizzanim Long-Term Ecological Research (LTER) Nature Reserve.

The mobile parabolic dunes have 5–15% perennial vegetation cover, which is mainly distributed on the dune crest and the slipface (windward vegetation cover is 3%, crest—20%, and slipface—32%, when normalized by the slope length resulting in 5–15% total cover). Maritime grass (*Ammophila arenaria*) is characteristic only to the mobile dunes and is the dominant perennial species along with wormwood (*Artemesia monosperma*). Fixed dunes have 31–50% perennial plant cover, which is distributed almost evenly across all slopes (38%, 44% and 46%, respectively). They are dominated by desert broom (*Retama racemosa*) and wormwood and have higher perennial plant species richness. They are the only...
dune state to have Mediterranean perennial species such as *Prasium majus* and *Asparagus horridus* [49].

2.2. Study Design and Fieldwork

The study was of a nested design: the patch scale was nested in the slope scale, which was nested in the dune scale. Six dunes were studied: three mobile dunes and three fixed dunes. We focused on annual plants as they are more susceptible to a wide spatial range of changes in soil and micro-climate properties compared to the woody perennial plants [50].

Annual plant observations were conducted during spring (March–April) in the years 2006, 2007, 2009, 2014, 2015 and 2016. For each dune, 72 quadrats of 40 × 40 cm were sampled per year, with 24 quadrats per slope aspect, 12 under the shrub and 12 in the open, adjacent to the observed shrubs. Quadrats were placed randomly but alternately into perennial bush or open patches within a 100 m² zone at the middle of each slope. The quadrats in the fixed dunes were placed only under *Artemisia monosperma*, a key species of the coastal sand dunes in the Levant [51], and in mobile dunes only under *Artemisia monosperma* and *Ammophila arenaria*, since these were the most common perennial species in the respective dunes. Annual plants were identified to species level, when possible, and their relative percentage cover was recorded at each quadrant.

2.3. Statistical Analysis

The effects of the environmental conditions (dune type, slope type and patch type) on total vegetation cover, species richness (i.e., number of observed species), beta diversity (i.e., distance to group centroid in ordination) and species assemblages were evaluated as follows:

1. Environmental effects on vegetation cover (first row in Figure 2) were evaluated by fitting mixed effects linear models with random effects of the dune identity (e.g., M1 = mobile dune #1, etc.) and sampling year (e.g., 2007) to take into account unmeasured sources of variation affecting plant cover across spatial locations and sampling time periods. Significance levels of differences between estimated marginal means of the groups were corrected using the Bonferroni method.

2. Environmental effects on species richness (i.e., count of unique species) (second row in Figure 2) were evaluated with the same approach as in case (1), only using mixed effects generalized linear models, with a Poisson distribution, instead of mixed effects linear models, since the dependent variable was the species count. Significance levels of differences between estimated marginal means of the groups were corrected using the Bonferroni method.

3. Environmental effects on beta diversity (third row in Figure 2) were evaluated using Anderson’s PERMDISP2 procedure for the analysis of multivariate homogeneity of group dispersions [52], where the distances of group members to the group centroid are subject to ANOVA. Samples were placed in multivariate space using the $\beta_t$ [53,54] measure of dissimilarity. Significance levels of differences between group means were corrected using Tukey’s “Honest Significant Difference” method.

4. Environmental effects on species composition were evaluated using redundancy Analysis (RDA) ordination (Figure 3), separately for each pair of groups being compared, followed by a permutation test to assess the significance of the constraints, corrected using the Bonferroni method.
Figure 2. Distribution of vegetation cover, species richness and beta diversity among samples, separately for each dune type (“Type”), dune type and slope combination (“Type + Slope”), and dune type and patch combination (“Type + Patch”) (M = mobile dune; F = fixed dune; W = windward; C = crest; S = slipface; O = open; B = bush).

Figure 3. Redundancy analysis (RDA) of species composition, constrained by dune type (top), dune type and slope type combinations (middle), or dune type and patch type combinations (bottom). Species scores are shown in red, site scores are shown in black. Sites belonging to each of the two groups being compared are marked with a convex hull polygon (M = mobile dune; F = fixed dune; W = windward; C = crest; S = slipface; O = open; B = bush, *** p < 0.001, ** p < 0.01, * p < 0.05, NS = not significant).
The latter four types of models, where the dependent variables were either (1) cover, (2) richness, (3) beta diversity, or (4) plant assemblage, were fitted separately for three “levels” of observation:

1. Comparing dune types,
2. Comparing dune type/slope combinations, and
3. Comparing dune type/patch combinations.

The results regarding the environmental effects on cover, richness, beta diversity and plant assemblages are summarized in Table 1 and visualized in Figure 2 (cover, richness and beta diversity) and Figure 3 (plant assemblages).

Table 1. Estimates and significance levels when comparing vegetation cover, species richness, species assemblages (i.e., species composition) and beta diversity, among dune types (“Type”), dune type and slope combinations (“Type + Slope”), and dune type and patch combinations (“Type + Patch”). The “Effect” column specifies the pairwise comparisons; for example, an M-F cover estimate of −10.43 means that vegetation cover was higher by 10.43, on average, for fixed dunes compared to mobile dunes (M = mobile dune; F = fixed dune; W = windward; C = crest; S = slipface; O = open; B = bush). (** p < 0.001, * p < 0.01, * p < 0.05, NS = not significant).

| Level          | Effect       | Cover  | Richness | Assemblages | Beta |
|----------------|--------------|--------|----------|-------------|------|
| Type           | M-F          | −10.43 | −0.90    | ***         | 0.01 |
| Type + Slope   | MC-FC        | −10.77 | −1.01    | ***         | *    |
| Type + Slope   | MS-FS        | −11.63 | −0.75    | ***         | *    |
| Type + Slope   | MW-MC        | −0.52  | −0.14    | NS          | 0.02 |
| Type + Slope   | MW-MS        | −1.32  | −0.44    | NS          | 0.03 |
| Type + Slope   | MC-MS        | −0.81  | −0.30    | NS          | 0.07 |
| Type + Slope   | FW-FC        | −2.44  | −0.20    | NS          | 0.04 |
| Type + Slope   | FW-FS        | −4.11  | −0.23    | NS          | −0.02|
| Type + Slope   | FC-FS        | −1.67  | −0.04    | NS          | 0.02 |
| Type + Patch   | MO-FO        | −15.26 | −0.81    | **          | 0.00 |
| Type + Patch   | MB-FB        | −5.66  | −1.03    | **          | 0.01 |
| Type + Patch   | MO-MB        | 1.08   | 0.41     | NS          | −0.02|
| Type + Patch   | FO-FB        | 10.68  | 0.18     | **          | −0.02|

Species turnover, when moving from mobile to fixed dunes, was calculated at three levels: considering the species assemblage in all samples combined, separately for samples from each slope type and separately for samples from each patch type (Figure 4). Species turnover was defined using the $\beta_i$ index, contrasting the complete list of species in mobile vs. fixed dunes [53].
Figure 4. Species turnover ($\beta_t$) of the transition from mobile to stabilized dunes, when considering the species composition in all samples combined (“Type”), separately in each slope type (“Slope”) or separately in each patch type (“Patch”) (M = mobile dune; F = fixed dune; W = windward; C = crest; S = slipface; O = open; B = bush).

Indicator species were identified using the indicator value method [55], using three levels of grouping of samples: by dune types, by dune type and slope type combinations and by dune type and patch type combinations (Table 2).

Table 2. Significant ($p < 0.05$) indicator species of dune types (“Type”), dune type and slope type combinations (“Type + Slope”), and of dune type and patch type combinations (“Type + Patch”) (M = mobile dune; F = fixed dune; W = windward; C = crest; S = slipface; O = open; B = bush).

| Level       | Ind. | Species                                                                 |
|-------------|------|-------------------------------------------------------------------------|
| Type M      |      | *Trisetaria koelerioides*                                               |
| Type F      |      | *Anagallis arvensis, Arenaria leptoclados, Asphodelus tenuifolius, Avena barbata, Brassica tournefortii, Bromus rigidus, Bromus sterilis, Campanula sulphurea, Daucus glaber, Erodium laciniatum, Galium aparine, Geranium robertianum, Hormuzakia sp., Lagurus ovatus, Lotus halophilus, Lupinus angustifolius, Lupinus palaestinus, Maresia pulchella, Ononis serrata, Phleum exaratum, Plantago sarcophylla, Rumex bucephalophorus, Rumex pictus, Torilis arvensis, Urospernum picroides* |
| Type + Slope MW |      | *Crepis aculeata, Cutandia memphitica, Trisetaria koelerioides*             |
| Type + Slope MC |      | *Cutandia memphitica, Trisetaria koelerioides*                             |
| Type + Slope MS |      | *Corynephorus articulatus, Crepis aculeata, Launaea fragilis, Lotus halophilus, Trisetaria koelerioides* |
| Type + Slope FW |      | *Asphodelus tenuifolius, Avena barbata, Brassica tournefortii, Bromus rigidus, Corynephorus articulatus, Crepis aculeata, Daucus glaber, Galium aparine, Hormuzakia sp., Lotus halophilus, Maresia pulchella, Rumex bucephalophorus, Rumex pictus* |
Overall, 77 annual plant species were identified across all samples. Out of the 77 species, three species were observed only in mobile dunes, 40 species were observed only in fixed dunes and 34 species were observed in both mobile and fixed dunes. We refer to

### Table 2. Cont.

| Level            | Ind. | Species |
|------------------|------|---------|
| Type + Slope FC  |      | Anagallis arvensis, Asphodelus tenuifolius, Avena barbata, Brassica tournefortii, Bromus rigidus, Campanula sulphurea, Corynephorus articulatus, Crepis aculeata, Cutandia memphitica, Daucus glaber, Erodium laciniatum, Galium aparine, Geranium robertianum, Hormuzakia sp., Lotus halophilus, Lupinus palaestinus, Maresia pulchella, Plantago sarcocephylla, Rumex bucephalophorus, Rumex pictus, Trisetaria koelerioides, Urospermum picroides |
| Type + Slope FS  |      | Anagallis arvensis, Arenaria leptoclados, Asphodelus tenuifolius, Avena barbata, Brassica tournefortii, Bromus rigidus, Campanula sulphurea, Corynephorus articulatus, Crepis aculeata, Daucus glaber, Erodium laciniatum, Galium aparine, Geranium robertianum, Hormuzakia sp., Lotus halophilus, Lupinus palaestinus, Ononis serrata, Rumex bucephalophorus, Rumex pictus, Trisetaria koelerioides, Urospermum picroides |
| Type + Patch MO  |      | Crepis aculeata, Ifoga sp., Lotus halophilus, Polycarpon succulentum, Trisetaria koelerioides |
| Type + Patch MB  |      | Launaea fragilis, Trisetaria koelerioides |
| Type + Patch FO  |      | Anagallis arvensis, Arenaria leptoclados, Asphodelus tenuifolius, Brassica tournefortii, Bromus rigidus, Bromus sterilis, Campanula sulphurea, Crepis aculeata, Daucus glaber, Erodium laciniatum, Galium aparine, Hormuzakia sp., Ifoga sp., Lotus halophilus, Lupinus angustifolius, Lupinus palaestinus, Maresia pulchella, Neurada procumbens, Ononis serrata, Phleum exaratum, Plantago sarcocephylla, Polycarpon succulentum, Rumex bucephalophorus, Rumex pictus, Torilis arvensis, Trifolium tomentosum, Trisetaria koelerioides, Urospermum picroides |
| Type + Patch FB  |      | Anagallis arvensis, Asphodelus tenuifolius, Avena barbata, Brassica tournefortii, Bromus rigidus, Campanula sulphurea, Crepis aculeata, Daucus glaber, Erodium laciniatum, Galium aparine, Geranium robertianum, Hormuzakia sp., Lagurus ovatus, Lotus halophilus, Maresia pulchella, Plantago sarcocephylla, Polycarpon succulentum, Rumex bucephalophorus, Rumex pictus, Sonchus tenerrimus, Urospermum picroides |

### 2.4. Software

All analyses were done using R [56]. Mixed effects linear models and mixed effects generalized linear models were fitted using the package lme4 [57]. Marginal means were estimated and pairwise-compared using the emmeans package [58] (Table 1). Beta diversity (Figure 2) was estimated through the \( \beta_1 \) index [53], using the function betadiver in the R package vegan [59]. Comparisons of beta diversity between dune types, between type/slope combinations and between type/patch combinations were done using the function betadisper in the R package vegan [59] (Table 1, Figure 2). Species turnover, also using the \( \beta_1 \) index via the betadiver function, was estimated when combining all samples from each dune type into a collective species list (Figure 3). Permutation tests on redundancy analysis (RDA) ordination were done using the package vegan [59]. Pairwise comparisons of groups in RDA were done using the function multiconstrained in the R package BiodiversityR [60] (Table 1, Figure 3). Indicator species identification (Table 2) was done using the package indicspecies [61].

### 3. Results

#### 3.1. Overview

Overall, 77 annual plant species were identified across all samples. Out of the 77 species, three species were observed only in mobile dunes, 40 species were observed only in fixed dunes and 34 species were observed in both mobile and fixed dunes. We refer to
each scale separately, comparing the differences among the studied landscape units within each scale. Thus, the contribution of each scale can be addressed separately to understand the process of dune stabilization from mobile dunes to stabilized dunes.

3.2. Dune Scale

Annual plant cover and species richness were significantly higher for fixed dunes compared to mobile dunes (Table 1, Figure 2). The plant assemblages also differed significantly between the two dune types (Table 1, Figure 3). Beta diversity did not significantly differ between dune types (Table 1, Figure 2).

The species turnover ($\beta_t$) value for the transition from mobile to fixed dunes was 0.39, given possible values between 0–1, where 0 indicates full similarity between two habitats and 1 indicates full dissimilarity (Figure 4).

*Trisetaria koelerioides* was classified as a significant indicator of mobile dunes, while 25 different species were classified as significant indicators of fixed dunes (Table 2).

3.3. Slope Scale

There were no significant differences between the slopes of the same dune type considering vegetation cover, species richness, assemblages and beta diversity, excluding a significant difference in species richness between the S (slipface) slope aspect and the W (windward) slope aspect of the two dune types. However, there were significant differences in cover, richness and assemblage composition between mobile dunes and the fixed dunes in each of the three slope aspects (Table 1, Figures 2 and 3). Beta diversity among samples did not significantly differ between any of the dune types and slope aspects combinations (Table 1).

The species turnover ($\beta_t$) for the transition from mobile dunes to fixed dunes, considering samples from each of the slope types, ranged between 0.42 to 0.44 (Figure 4).

When considering dune type and slope type combinations, 13 indicator species were identified for W slopes, 22 species for C (crest) slopes and 22 for S slopes on fixed dunes, while only three, two and five species were identified as indicators of W, C and S slopes on mobile dunes, respectively (Table 2).

3.4. Patch Scale

Open patches were significantly different from patches beneath the shrubs in terms of vegetation cover (only in stabilized dunes), species richness (in both dune types) and assemblage composition (only in fixed dunes) (Table 1, Figures 2 and 3). Fixed dunes differed from mobile dunes in terms of vegetation cover, species richness and assemblage composition (Table 1, Figures 2 and 3). Beta diversity among samples did not significantly differ between any of the dune types and patch type combinations (Table 1, Figures 2).

The species turnover ($\beta_t$), for the transition from mobile to stabilized dunes, was 0.47 when considering samples from bush patches and 0.42 when considering open patches (Figure 4).

When considering dune type and patch type combinations, 28 indicator species were identified for open patches and 21 species for bush patches on fixed dunes, while only five and two species were identified as indicators of open and bush patches on mobile dunes, respectively (Table 2).

4. Discussion

4.1. Overview

Most studies on the dune stabilization process have focused on the dune scale, using the changes in perennial vegetation cover and its spatial pattern. These two measures have a significant direct correlation with dune stabilization [18,35,41]. The increase of perennial vegetation cover is followed by changes in soil properties, namely a decrease in sand mobility [35,47] and increase in soil silt and clay content [14,62], soil organic matter [13,23], soil nutrients [36] and soil moisture [13]. Therefore, the perennial plants are considered
as ecosystem engineers that are responsible for the changes in the physical and geomorphic dune state from a mobile to a fixed state, thus increasing spatial heterogeneity [19]. Annual plants are facilitated by the perennial plants, which determine their composition and spatial distribution [13,49,50]. In contrast to perennial plants, annuals are more sensitive to micro-spatial and temporal changes. Annual plant compositions and their morphological and phonological properties change over small distances, sometimes even of a few centimeters, due to micro environmental changes. Perennial plants have strong impacts on the adjacent open patches, as well as the area under their own canopy—especially on sand dunes where the substrate mobility is very crucial for the plants’ micro-scale [13,50,63]. Thus, annual plants represent the fine grain of the plant community scale.

4.2. Dune Scale

The transition from mobile dunes to fixed dunes is followed, as expected, by a significant increase in annual vegetation cover and species richness and a significant change in plant assemblages. The $\beta$ species turnover, which indicates the percentage of similarity between the assemblages based on species presence/absence, was only 0.39. Only one species, *Trisetaria koelerioides*, was found to be an indicator species for mobile dunes. The Sandiness Index [41] of this species is 0.91, with index values ranging between 0 and 1, where 1 indicates the highest affinity of an annual (organism) species to mobile sand dunes. In turn, 25 indicator species were identified for fixed dunes, whereas the Sandiness Indexes for 19 species were very low due to the fact that these species can also be found in other Mediterranean habitats and not only on sandy soils. In order to assess the assemblage affinity towards mobile dunes or the similarity to mobile dune assemblages, we developed the Dune Assemblage Index (DAI) [41]. This index, calculated per dune, ranges between 0–1, where a DAI of 0 represents an assemblage in which the species are restricted to fully fixed dunes and a DAI of 1 represents an assemblage in which the species are restricted to fully mobile dunes. The average of the Dune Assemblage Index for mobile dunes at the present research site, based on annual plants, was found to be 0.66, and a score of 0.36 was found for the fixed dunes. To summarize, observations on the dune scale suggest that the transition from mobile to fixed dunes is followed by significant changes in annual plant cover, richness and composition.

4.3. Slope Scale

There were no significant differences in plant cover and assemblages between the different slope types within both dune types. The only detected difference was in the number of species, which was significantly higher in the slipface slopes compared to the windward slopes. The environmental conditions at the mobile dunes are harsh [14,17,38]: the windward slope is subject to sand erosion while the slipface is affected by sand deposition. The perennial plant cover is very low and distributed mainly at the crest and slipface slopes in a clumped pattern [35,39]. The perennial plant cover of the fixed dunes is higher than that of the mobile dunes, but almost uniform across all the slope aspects due to the improvement in the physical environmental conditions [12,50]. Still, the cover on the windward side is slightly lower compared to the other two slope aspects, probably because there is still some sand movement at the windward slope.

Comparing dune types separately for samples taken from each of the three slope types indicated that the annual plant cover, the number of species and the plant assemblages significantly differ between dune types. The $\beta$ species turnover ranges between 0.42–0.44; i.e., there was a similarity level of about 40% among dune types, considering the various slope types.

4.4. Patch Scale

One of the most limiting factors for annual plants in the Mediterranean is light [64]. Therefore, we expect to find these plants mostly at the open patches. Moreover, the hydraulic conductivity at the dune open patches is much higher (in our case five times
higher) than beneath the shrub due to the coarse texture, and absence of organic matter and allelopathic effect [35]. Therefore, higher soil moisture is available for annual plants at the first 30 cm of soil depth during the rainy season [50].

In both dune types, the number of species in the open patches was significantly higher than beneath shrubs. However, only on the fixed dunes was the difference also expressed by higher cover and different species assemblages.

4.5. Synthesis

Combining the dune, slope aspect and patch scales provides a more complete picture of the processes underlying changes in annual vegetation during dune stabilization, since different processes take place at different scales and stages. The transition from mobile to fixed dunes is characterized by the expansion of annual vegetation mainly in the slip-faces, which are relatively protected from the wind, and by the re-equalization of annual vegetation cover and species number at the patch scale. The annual vegetation cover and species number increase in both shrub and open patches, but in the latter more than in the former. The perennial plants have a stronger net facilitative effect within some distance from their canopies due to wind sheltering, while under their canopy, they have a stronger net negative effect due to competition for water and allelopathy, among other factors [40,65–71].

4.6. Implementation for Biodiversity Conservation

The dune stabilization process under a Mediterranean climate in the Eastern Mediterranean Basin, with a low drift potential, is characterized by significant geomorphological and ecological changes taking place over a period of 40–60 years [16,17]. These changes comprise the transition from parabolic dunes to fixed dunes and from perennial and annual plant assemblages composed of psammophile, desert and endemic plant species to assemblages characterized by species with high Eastern Mediterranean affinity [13,50]. In order to conserve the spatial heterogeneity simultaneously composed of mobile and stabilized dunes, it is necessary to manage the dune ecosystem by the remobilization of a certain part of the stabilized dunes. Principally, the idea sounds simple and coincides with conclusions obtained in numerous studies regarding plant succession in sand dunes (for example, [12]). However, practically, the situation is much more complicated. A study conducted on the dunes studied here for 12 years, tracking plant re-establishment on fixed dunes, from which the perennial plants were removed, showed that treatment had very little effect on the plant community. Stronger response was found in semi-fixed dune treatments, in particular for mobile dune indicator species, which showed evidence of recolonization within a few years following treatment. However, it was concluded that only long and continuous disturbance pressures, such as grazing or even controlled 4 × 4 vehicle activity, could lead to the desired impact [20].

5. Conclusions

We have demonstrated how entity-defined multi-scalar analysis can promote ecological understanding by integrating the unique data and knowledge that can be acquired at each scale. In this study, we followed the changes in the annual vegetation during dune stabilization on three distinct scales. Starting with the dune scale, which is the most commonly studied, we identified the general trend of increasing annual vegetation cover and species number and the change in plant assemblages during dune stabilization. When making observations on the dune scale, little could be said about processes, except for postulating that annual plants establish more successfully when perennial vegetation cover increases and wind drift potential decreases. Analysis at the slope scale revealed that stabilization does not occur evenly among the morphological units of the dune. Since annual vegetation patterns are known to be associated with exposure to wind, these patterns served as concrete evidence for the facilitative effects of perennial plants in reducing exposure to wind. Analysis at the patch scale revealed that the perennial plants also have
negative effects on the annual vegetation, but that these negative effects operate at different scales, magnitudes and spatial distribution than the facilitative effects. Integrating these three scales provided a more detailed, complex and realistic picture of the processes that annual vegetation undergoes during dune stabilization.

**Author Contributions:** P.B.K.: Conceptualization, methodology, validation, formal analysis, investigation, resources, data curation, writing—original draft preparation, writing—review and editing, supervision, project administration, funding acquisition. M.D.: Software, validation, formal analysis, investigation, data curation, writing—original draft preparation, writing—review and editing, visualization. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by the Israeli Nature and Park Authority.

**Institutional Review Board Statement:** Not applicable.

**Informed Consent Statement:** Not applicable.

**Data Availability Statement:** The data presented in this study are available on request from the corresponding author. The data are not publicly available due to being part of a large database used by the project for various research purposes.

**Acknowledgments:** We wish to thank the Israeli Nature and Park Authority for financing this project, the undergraduate and graduate students who did the field work and Tania Bird for organizing the data.

**Conflicts of Interest:** The authors declare no conflict of interest.

**Abbreviations**

The following abbreviations are used in this manuscript:

- M Mobile (dune)
- F Fixed (dune)
- W Windward (slope)
- C Crest (slope)
- S Slipface (slope)
- O Open (patch)
- B Bush (patch)

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