

Variation between bee communities on a sand dune complex in the Great Basin Desert, North America: Implications for sand dune conservation

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ABSTRACT

Sand dunes across the Mojave and Great Basin Deserts house rich bee communities. The pollination services these bees provide can be vital in maintaining the diverse, and often endemic, dune flora. These dune environments, however, are threatened by intense off-highway vehicle (OHV) use. Conservation efforts adopted by land managers often consist of setting aside a portion of a dune system that is off-limits to OHV use, but little work has been done showing the extent to which this protects native bee communities. A two-year study of bee communities on a Great Basin sand dune complex in Dugway Proving Ground located in northwestern Utah revealed low similarity index values between closely situated collecting plots (1–40 km apart). Similarity values ranged from 0.13 to 0.70 for species composition, and from 0.07 to 0.57 when similarity was weighted by abundance. Distance between plots had no significant relationship to similarity when richness and abundance were considered. Bee similarity between plots was significantly correlated with floral similarity. These results indicate that dune conservation strategies that preserve “representative” portions of dune systems may be insufficient to protect bees and the pollination services they provide.

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1. Introduction

In contrast to the general global pattern of increasing species diversity as one approaches the equator, bees (Hymenoptera: Apiformes) are most diverse in the world's deserts and Mediterranean regions, including the southwestern United States and adjacent Mexico (Michener, 2000). Not all desert landscapes, however, support equally diverse bee faunas. In the Basin and Range Province of the western U.S., dune environments support a larger bee fauna than the neighboring bajadas and playas (e.g., Toler, 2001). Sand dunes provide more available water after rain than do many other desert soils (Tsoar, 1990), and as a result, support a relatively rich flora (Pavlik, 1985). Dunes also offer a unique loose nesting substrate and an attractive alternative to the alkaline soils that often surround them (Cane, 1991).

In the Great Basin Desert, sand dunes are rare habitats (Holland et al., 1999). Due to their dynamic nature, they are sensitive to disturbance. Studies worldwide have shown the generally negative

effects of anthropogenic activity on the dune biota (e.g., Luckenbach and Bury, 1983; Schlacher and Thompson, 2008). Bees may be particularly vulnerable to the effects of off-highway vehicles (OHVs) because of their resource requirements. Bees require two main resources: 1) pollen and nectar both for provisioning nest cells and for sustenance, and 2) appropriate nesting substrate or other nest-building materials. OHV use can negatively impact floral resources on dunes, as well as nesting habitats. The resource requirements of bees are often extremely specific. Pollen collection may be limited to only one or a few closely related plant genera (and in some cases species) (Cane and Sipes, 2006). With a few exceptions, bees do not fly long distances (Greenleaf et al., 2007), tending instead to nest in an area centrally located amongst floral resources (Tinbergen, 1951). If dune-restricted plants are a large component of a bee's diet, OHV activity that destroys these floral resources can be expected to negatively impact bee populations (Stebbins, 1995). Even moderate OHV traffic significantly reduces native plant cover (Groom et al., 2007). Additionally, the disturbance of stabilized dunes by OHVs promotes the establishment of invasive species such as cheat grass (*Bromus tectorum* Linnaeus), often at the expense of native plant resources upon which insects depend (Sheffield et al., 2003).

Of even greater consequence, destruction of bee communities may have disproportionate consequences for dune ecosystems as

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a whole (Gottsberger et al., 1988) because of the vital pollination services bees provide (Proctor et al., 1996). Many bees found on sand dunes are specialist pollinators, meaning they pollinate a limited variety of plants (Proctor et al., 1996). In many instances, specialist bees are more efficient pollinators of their host plants than generalist pollinators (Cane and Payne, 1988; Tepedino, 1981). Healthy bee communities are, therefore, a crucial component of a healthy dune system. For example, the availability of effective pollinators is the main limit on seed production for two highly endangered plants on a dune complex in Central California (Pavlik et al., 1993). Because many plants rely on bees for pollination, bees are considered keystone components of almost all terrestrial ecosystems (Sheffield et al., 2003).

Few studies have addressed the issues associated with the maintenance of diverse bee faunas outside of agricultural environments (James and Pitts-Singer, 2008), and none in the context of dune systems. Currently, the compromise often proposed for dune conservation is to set aside large regions that are off-limits to OHVs while leaving the remainder of the dunes open (e.g., Little Sahara Recreation Area, Utah; Coral Pink Sand Dunes State Park, Utah; Algodones Dunes, California). The extent to which this management strategy effectively preserves species diversity, however, is a subject of debate (e.g., Groom et al., 2007; Wright et al., 2001). Previous studies have shown that some organisms exhibit uneven distributions across seemingly homogeneous dune landscapes (Barrows and Allen, 2007), but no studies have investigated spatial patterns of bee communities on dunes. Considering the spatial and temporal variability of bee communities found in other landscapes (Griswold et al., 1998; Messinger, 2006), and the key pollination services bees provide, conservationists must account for this heterogeneity when outlining areas to protect.

Dugway Proving Ground (DPG), located in northwestern Utah, is home to an extensive dune system that is relatively undisturbed because of limited public access, making it one of the most important protected areas in the Great Basin Desert (Holland et al., 1999). DPG also supports a diverse bee fauna (Toler, 2001; Wilson et al., 2008). For these reasons, DPG provides an ideal laboratory to document the natural variability of dune bee faunas.

Here we investigate the intra- and inter-dune variability of bee communities in an intact dune environment through time. We address three specific questions: 1) Does bee diversity (richness and abundance) differ between regions of a dune field? 2) Do different areas of the dune harbor unique bee faunas (and if so, is it a result of the floral composition)? 3) Is temporal variability (between years) in bee community composition less than spatial variability? While we make no assertions as to best management practices for dune environments, our results can provide insight into the possible repercussions of choosing single areas or habitat types when setting aside areas for conservation.

2. Materials and methods

2.1. Study area

Until 14,000 years ago, DPG was almost entirely submerged beneath Lake Bonneville (Oviatt et al., 2003). Dunes formed from the lacustrine deposits left after the lake level dropped, often between the margins of receding lakes and mountain ranges (Oviatt et al., 2003). At present, there are at least five distinct dunes in DPG, separated by alkaline flats or gravel bars (Fig. 1). All dunes occupy a similar elevation. While gypsum dunes do exist in DPG, the dune fields used in this study are siliceous, and do not differ substantially in composition. Each of the dunes has areas of open sand; however, the dunes are relatively stable and are largely vegetated.

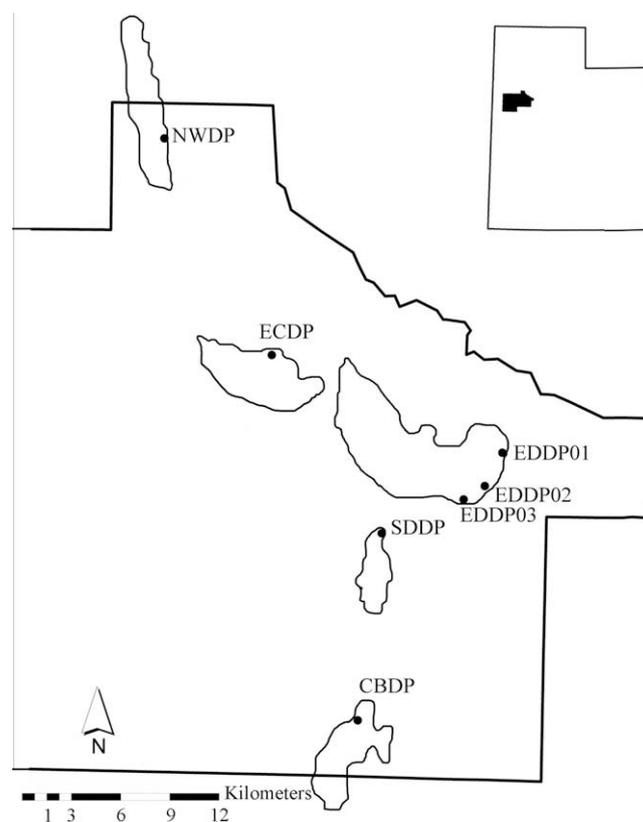


Fig. 1. Map of the sand dunes in Dugway Proving Ground, Utah, with locations of sampled plots labeled and the boundary of the proving ground marked.

In 2003 we explored intra-dune bee distributions across the largest dune in DPG, the East Dugway Dunes (EDD), utilizing standardized plots in three different locations (Fig. 1). One hectare plots (100 m × 100 m) were laid out using Garmin 12XL GPS units and flagged at the corners and center to aid collectors in orientation. Plots were separated by 1–3 km. Locations were limited to areas where recreational off-highway vehicle travel was prohibited. The three plots on EDD were established in vegetated areas, or in open dune areas with scattered vegetation. Dominant plants were similar between plots, but their abundance was variable. The presence of other plants, mainly annuals, was notably different between plots. Dominant vegetation included primrose (*Oenothera* spp.), sunflower (*Helianthus* spp.), money buckwheat (*Eriogonum nummularia* Jones), and rabbitbrush (*Ericameria* spp.). One plot included several Utah junipers (*Juniperus osteosperma* (Torr.) Little). In 2005, four plots on other dune fields were added in order to explore inter-dunal variability (Fig. 1). Plots were established in areas where dominant vegetation approximated that of the plots set up in 2003, and were within 40 km of each other. The habitat type of each plot was determined to be either open dune, partially vegetated dune, or vegetated dune (Table 1).

2.2. Sampling design

Collecting began in early May and continued bi-weekly through September. Plots were sampled using a combination of pan traps (colored plastic bowls) and nets according to a standardized protocol (LeBuhn et al., 2003). Two lines of 15 pan traps (in total 10 each of fluorescent blue, fluorescent yellow, and white) filled with soapy water were evenly spaced along the diagonals of the plot between opposite corners, thus dividing the plot into 4 isosceles

Table 1
Site characteristics for 1 ha plots located on sand dunes in Dugway Proving Ground, UT. (–) indicates that the plot was not collected in that year. Richness and abundance are based on six collecting events over the course of a field season, chosen at random from the total number of collecting events during that field season for a plot, averaged over a thousand runs. Standard deviations are for the thousand runs and indicate the range of values possible from the runs.

Plot	Bee richness (SD)				Bee abundance (SD)				Habitat type
	2003		2005		2003		2005		
EDDP01	39.19	(5.58)	29.40	(4.93)	277.69	(50.68)	273.84	(60.11)	Open dune
EDDP02	26.04	(2.87)	43.53	(6.01)	485.93	(92.37)	678.19	(228.83)	Vegetated
EDDP03	41.94	(5.23)	50.06	(5.09)	886.89	(179.73)	980.58	(338.46)	Vegetated with juniper
SDDP	–	–	44.00	(5.06)	–	–	478.21	(193.31)	Vegetated
CBDP	–	–	39.11	(5.22)	–	–	596.91	(167.71)	Partially vegetated
ECDP	–	–	42.37	(3.33)	–	–	392.26	(37.47)	Partially vegetated
NWDP	–	–	37.00	(0)	–	–	372.00	(0)	Open dune

triangles. Pan traps were deployed before 9:00 and collected after 16:00, thus spanning the period of flight for most bees. In 2005 we used smaller pan traps (96.1 ml) than in 2003 (236.5 ml); there is no statistical difference in capture between trap sizes (Droege, 2005). In addition to pan traps, two collectors simultaneously sampled each plot with nets twice per bi-weekly visit. Plots were sampled once before 12:00 and once after 12:00. Bees were collected in plots for 30-min periods, with time divided equally among the 4 quadrants of the plot. An effort was made to capture bees on all plants blooming at the time of collection.

All collected bees were labeled and identified to species, with the exception of male specimens of *Lasioglossum (Dialictus)*; there is no revision of this group and the association of sexes is not possible. Specimens are deposited at the USDA-ARS Bee Biology and Systematics Laboratory (BBSL) in Logan, Utah with a synoptic set returned to DPG.

2.3. Analytical methods

Beta diversity, or spatial turnover in community composition, is evaluated with any number of indices. Bray–Curtis is a common metric that can be computed using either presence/absence data, or raw abundance data (Bray and Curtis, 1957; Southwood, 1978). Similarity values between plots were calculated using PC-ORD version 4.34 (McCune and Mefford, 1999). Bray–Curtis values range from 0 to 1, with one indicating two faunas that are congruent in either composition (presence/absence) or composition and abundance (raw abundance data). Similarity values for 2003 and 2005 were calculated separately, based on cumulative species counts for each plot across the season. Military maneuvers and other restrictions prohibited some scheduled bi-weekly samples, resulting in an uneven number of collecting events (plot-day) across plots. Comparisons between plots collected at different frequencies would lead to inaccurate similarity values. Therefore, we used sample-based rarefaction, whereby N collecting events (samples) are drawn from the total pool of all visits to a site (Colwell and Coddington, 1994; Simberloff, 1978), with N being equal to the number of visits to the least-visited plot (6). The cumulative results after N draws were used for calculations of abundance, species composition and similarity. Draws were repeated 1000 times and averaged. Similarity values were also calculated for flowering plant species composition between plots sampled in 2005. Unless otherwise stated, all values presented are based on our sample-based rarefactions, and do not represent absolute diversity for a plot.

To assess whether differences in similarity were a result of distance between sites (Nekola and White, 1999), we applied a Mantel test (PC-ORD 1000 randomizations) to the Bray–Curtis ‘distance’ matrix (calculated similarity values) and a between-plots distance matrix.

3. Results

3.1. Does bee diversity (richness and abundance) differ between regions of a dune field?

Plot samples yielded 9579 specimens during the 2003 and 2005 field seasons. This represents 163 species (2003: 108; 2005: 123; absolute), 31 genera, and all six North American bee families. Based on the average of six randomly drawn collection days (see Methods section), plots differed significantly in terms of both richness and abundance across the season (Table 1). Specifically, all plots differed significantly from each other ($p < 0.0001$, Bonferroni adjusted) in 2005 except for SDDP and EDDP02 in terms of richness, and ECDP and NWDP in terms of abundance. In 2003 all plots also differed significantly in terms of richness and abundance ($p < 0.0001$, Bonferroni adjusted). The most abundant species in DPG were highly localized (Fig. 2). Plots where many specimens were collected were not always equally species rich (Table 1). In 2005 open dune plots had significantly fewer bee individuals and lower richness ($p < 0.001$ for both abundance and richness) than semi-vegetated or wooded dunes.

3.2. Do different areas of the dune harbor unique bee faunas?

Many species’ distributions were restricted. Over a third (35%) of species represented by more than 20 specimens were localized, with more than 50% of individuals collected at one site. Moreover, the dominant species in each plot differed significantly, and never did the same five species account for the majority of collected specimens (Fig. 2).

Whether using abundance or presence–absence data the results suggest an exceedingly variable landscape, where communities, even on the same dune fields, are highly dissimilar (Table 2). Similarity values calculated using only presence/absence data range from 0.10 to 0.70, a greater range than values that included abundance data (0.10–0.52). The least similar plots in 2005 were EDDP02 and NWDP. The greatest similarity in both 2003 and 2005 (EDDP02 and EDDP03) was surprisingly low given their proximity (1 km) and the near identity of their floral composition (Table 3).

The flora of plots were more similar to each other overall than the bee fauna between plots (average floral similarity using presence–absence data: 0.58; average faunal similarity using presence–absence data: 0.44; t test: $t = 2.538$, $p = 0.022$) (Table 3). Moreover, the similarity of floral resources was positively correlated with the similarity of bee faunas, both in terms of species composition ($R^2 = 0.61$, Mantel test: $p < 0.001$, 1000 permutations) and in terms of abundance ($R^2 = 0.662$, Mantel test: $p = 0.007$, 1000 permutations). Distance between plots was not associated with the similarity of plots based on either bee species composition or abundance (Mantel test, 1000 permutations).

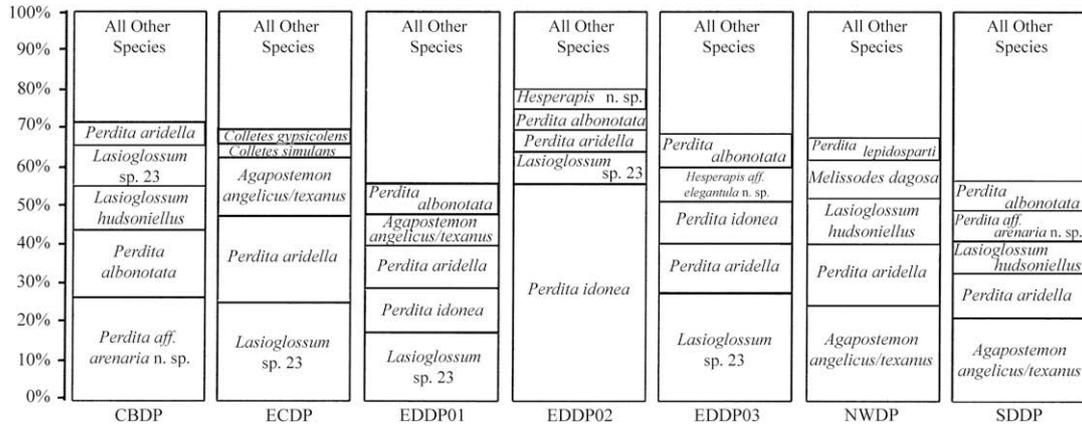


Fig. 2. Proportion of overall fauna represented by top five most abundant species, for each pot in 2005.

3.3. Is there more variability in bee community composition within one year between sites, or between years in the same site?

Similarity between years for the same site was relatively high when considering only presence/absence (EDDP01: 0.54, EDDP02: 0.49, EDDP03: 0.58). The abundance of different species, however, varied tremendously between years resulting in low similarity values when incidence was included (EDDP01: 0.31, EDDP02: 0.37, EDDP03: 0.34). When comparing a plot in one year to each of the plots from the other year (e.g., EDDP01 in 2003 to EDDP02 and EDDP03 in 2005), similarity values were consistently lower than values of a plot compared to itself. In other words, the faunal composition of a plot changed independently of other plots between years.

4. Discussion

Landscapes, including dunes, are never homogeneous (Barrows and Allen, 2007). There is therefore a question of size and number of replicates necessary to optimally represent alpha and beta diversity (Soule and Simberloff, 1986). Britten and Rust (1996) demonstrated that dunes located in different pluvial lake basins in the Mojave and Great Basin Deserts support genetically isolated populations of a dune obligate beetle (*Eusattus muricatus*). After finding that dunes separated by 100 km maintain genetically

distinct populations, they suggested these should be managed accordingly. Our data support their conclusion that diversity, genetic or specific, may be lost when one large representative area is conserved at the cost of smaller areas. Simply setting aside a single large area may be insufficient to preserve species diversity (Groom et al., 2007; Wright et al., 2001). Moreover, it has been shown that areas with high beta diversity, as we observed in DPG, may benefit most from conservation strategies that set aside several small reserves (Wiersma and Urban, 2005). However, if temporal turnover is high, as we also observed in bee populations in DPG, the long-term efficacy of many small reserves may be negligible (Fagan et al., 2001).

Many authors have shown that dunes support a diverse and distinct biota (e.g., Hardy and Andrews, 1979; Pavlik, 1985), and the frequency with which they are subjected to major conservation initiatives is an obvious consequence (Cordell et al., 2008). Land managers must choose from numerous strategies when designing reserves in order to meet any number of ecological objectives. For example, management goals may be met by preserving ecosystem function, biodiversity, unique species, genetic diversity, or keystone species (Pressey et al., 1993; Sundell-Turner and Rodewald, 2008). Because of bees' key role in the reproductive success of many plants and their high biodiversity on dunes, including many obligate psammophiles, it would be pertinent for conservationists to consider bee communities when designing reserves. Given that sand dunes provide critical resources for bees, and bees provide vital pollination services to plants both on and off the dunes, protecting a diverse bee community may be pivotal in the maintenance of a healthy dune system. Those interested in preserving bees and their pollination services in a dune landscape should consider three properties of bees in this environment.

First, our study indicates that species composition differs significantly between plots (Fig. 1). Whether between years or between plots within 3 km of each other, bee richness and abundance varied considerably. This characteristic is not unique to bees

Table 2
2005 similarity values for bees between plots. Bray–Curtis values including abundance and are located above the diagonal; similarity values calculated with species composition only and are located below the diagonal.

	Similarity values calculated with abundance						
	EDDP01	EDDP02	EDDP03	CBDP	ECDP	NWDP	SDDP
EDDP01	-	0.27	0.39	0.34	0.37	0.26	0.39
EDDP02	0.51	-	0.57	0.44	0.36	0.07	0.36
EDDP03	0.52	0.7	-	0.57	0.51	0.10	0.51
CBDP	0.48	0.56	0.57	-	0.51	0.10	0.52
ECDP	0.48	0.52	0.55	0.55	-	0.13	0.47
NWDP	0.24	0.13	0.15	0.19	0.14	-	0.14
SDDP	0.46	0.59	0.65	0.62	0.58	0.17	-

Table 3
2005 similarity values between plots, calculated with plant species composition.

	EDDP01	EDDP02	EDDP03	CBDP	ECDP	NWDP	SDDP
EDDP01	-	0.50	0.46	0.32	0.57	0.60	0.36
EDDP02		-	0.94	0.76	0.50	0.50	0.75
EDDP03			-	0.84	0.54	0.46	0.82
CBDP				-	0.61	0.32	0.84
ECDP					-	0.57	0.62
NWDP						-	0.36
SDDP							-

in dune habitats. Many other studies found spatially and temporally variable bee communities in a variety of landscapes (Griswold et al., 1998; Messinger, 2006). While the reasons for this variability are unclear, there is little doubt that the source–sink dynamics suggested by this pattern need to be considered when delineating areas for conservation.

Second, community composition varies significantly between locations, and even the most abundant species in DPG are irregularly distributed. Both measures of beta diversity indicate that the assemblage of bee species at a site is unique. The fact that our presence/absence index indicates low similarity means that the difference between plots cannot be attributed solely to species abundance. Floral specialists (e.g., *Perdita subfasciata* and *Melissodes bimatrix*: *Chrysothamnus*; *Hesperapis carinata* and *Melissodes agilis*: *Helianthus*; *Osmia titusi*: Fabaceae), sand dune obligates (e.g., *Megachile* n. sp., and *Anthidium rodecki*), and cleptoparasites contributed significantly to spatial turnover. The prominence of these guilds in creating community variability has important implications. Endemics and specialists have been shown to be more susceptible to disturbance than ubiquitous generalists (Henein et al., 1998). Rare species, such as cleptoparasites, are also particularly prone to extinction (Volkov et al., 2003). Finally, species with skewed spatial distributions, such as many of the more common species in DPG, are more vulnerable to local extinction than species with an even distribution across a landscape (Hanski, 1998).

The reasons for heterogeneity on a seemingly homogeneous landscape are unclear. Brosi et al. (2008) found that the considerable beta diversity between sites in southern Costa Rica could be explained by habitat. While overall habitat type (vegetated, partially vegetated, and open dune) did not correspond to the similarity of bee faunas, floral assemblages seem to affect bee similarity. Floral similarity was significantly correlated with bee similarity. While the dominant plants were common in most plots, the presence of other flowering plants was not homogeneous. The connection between bee similarity and floral similarity may be explained in part by specialist bees that only occur where particular plants do. Several of the plants on which these bees specialize are key components of the flora where they occur. Additionally, the presence of *J. osteosperma* in EDDP03 may have provided nesting sites for cavity-nesting bees whose distribution is restricted to areas with suitable woody material (Potts et al., 2005), though EDDP03 did not harbor more cavity-nesting bees than the other plots.

Finally, abundance and even presence of species differs between years for the same plot. The dominant plants in our plots were perennials that bloomed consistently in both years. In contrast, the bee fauna differed significantly in terms of both membership and abundance across years. Tepedino and Stanton (1981) found similar variability in bees at two sites in a Wyoming short-grass prairie habitat. Bee populations also appear to be spatially independent. This, too, is not unique to dune bees (Steffan-Dewenter and Schiele, 2008). The reasons for this lack of synchrony are unclear, but may include low dispersal rates for small insects (Greenleaf et al., 2007), or responses to local floral resources (Schaffers et al., 2008).

While it is not practical to implement dune conservation policies based solely on the population dynamics of one taxonomic group, our research does provide empirical evidence of spatial heterogeneity in at least one group that provides a vital ecosystem service in a fragile landscape. Moreover, it warrants research examining in greater depth the temporal aspects of heterogeneity of pollinator populations, and interactions that may exist between spatial and temporal dynamics. While our data can neither support nor refute decisions made concerning how best to conserve habitats shared by many user groups, it can inform land managers of the possible consequences of setting aside just one large area of a dune complex.

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