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BIODIVERSITY AND POLLINATION BIOLOGY OF BEES IN COASTAL NATURE PRESERVES.

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Abstract. Biodiversity (number of species and composition) of bee communities at the Lanphere-Christensen Dunes Preserve near Arcata, CA and Bodega Marine Reserve near Bodega Bay, CA is compared and contrasted. Differences in habitat (dunes and adjacent woodlands versus grassland, bus lupine, dunes, midden mounds, coastal bluffs), flowering plant communities, early and late season bee faunas, and specialization of bees for pollen collection from specific plants influence the diversity. Reproduction of many flowering plants depends on pollination by bees. Bees nest in habitats often removed from the primary flowering plants they pollinate. Since some plants appear to be pollinator limited this necessitates preservation of mosaics of habitats that include bee nest sites when developing management plans for conservation of flowering plants of concern.

Introduction

The word bees brings to mind in most people the honey bee. A few may recognize that bumble bees are somehow related, but even many entomologists are unaware of the tremendous diversity of bees. The world bee fauna of bees (superfamily Apoidea) is estimated at 20,000 species. Of these, about 10% are social, 75% are solitary, and 15% are cuckoo parasites of other bees (Bohart, 1970). Bees are most diverse and abundant in arid warm temperate areas of the world, especially in the Mediterranean, California, and adjacent desert areas (Michener 1979). With rare exceptions, bees rely on nectar and pollen as food resources: nectar primarily as energy for flight and other activities, pollen as nutrients for reproduction (ovarian and brood development). Most bees are generalists when foraging for nectar, restricted primarily by body or tongue size. Many bee species, however, exhibit host-specificity (oligolecty) in relation to pollen resources (Robertson, 1925; Linsley, 1958). Linsley and MacSwain (1958) define oligolecty as the collection of pollen from one or a few closely related plant species by all members of a bee species with use of alternative sources occurring only during stress periods when such pollen sources are locally (or temporarily) absent.

Bees are "keystone" species in most plant communities because of their importance as pollinators for the reproductive continuity of many flowering plants including rare and endangered species. This has not received the attention it deserves when formulating policies for conservation and mitigations (Tepedino, 1979; Thorp, 1990). Conservation activities often focus on preservation of the plant species, its habitat, or on restoration by transplanting seeds or seedlings. However, many of these same plants are dependent on bees which live in adjacent, but different habitats as defined by soil type and/or vegetation. Thus, the bees may not be protected or included in transplantings. Many plants, including rare and endangered species are pollinated by bees that are host-specific for pollen (Moldenke, 1976a, b; Tepedino *et al.*, 1990). These specialists may be more efficient pollinators than generalist species (Strickler, 1979). Conservation and restoration biologists will require better understanding of diversity in bee communities, bee/flower associations, and bee nest site requirements for habitat and continuation of bee pollinated plant populations.

Methods.

Biological inventories of bees, their host-plant associations, nesting habitats, and biologies were conducted at the Lanphere-Christensen Dunes Preserve (LCDP), Arcata, California (The Nature Conservancy) (Gordon, 1984) and the Bodega Marine Reserve (BMR), Bodega Bay, California (University of California, Natural Reserve System). Both sites are in the northern humid plant climate zones of California (Kimball, 1959) and the Temperate Mediterranean eco-floristic subzone (Barbour et al., 1975). Voucher specimens of bees were collected throughout the active season to determine species diversity, phenology, and flower associations. Nest site habitats were located for many bee species and nests were excavated for some to obtain nest architecture and additional life history information.

The relative abundance of bees at Bodega and Arcata dunes was based on relative numbers of voucher specimens collected and observations of bee abundance at the peak of their active season. Bees were rated as: Rare <5; Uncommon 5-10; Occasional 11-25; Common 26-50; Abundant >50.

Calculations of difference and resemblance among bee faunas and floras of the two sites are based on those used by Thorp *et al.* (1983). Difference = number of taxa not shared / sum of taxa X 100, thus, 0 = no difference and 100 = total difference. Resemblance = number of shared taxa / number of taxa in smallest fauna or flora X 100, thus 0 = no taxa shared and 100 = all taxa from smaller fauna or flora occur in the larger.

Six biogeographical patterns were recognized: 1) Holarctic and transcontinental in North America; 2) transcontinental, mostly Alaska, southern Canada and northern US; 3) western North America, mostly montane and intermountain areas west of 100 degrees longitude; 4) Pacific Coast area from British Columbia, Canada to northern Baja California, Mexico; 5) California with some limited to the coastal area; and 6) European introductions.

Analyses and comparisons of floras were based on floral surveys by Barbour (1970, 1972) at BMR and by Barker (1976) at LCDP. Data on bee visited flowers were obtained from personal observations.

Results

The bee faunas of Bodega and Arcata dunes are similar in numbers of families, genera and species (Table 1). The same six families occur at both sites, but only 18 of 27 genera and 22 of 68 species are shared. The relative abundance ratings show the rare to occasional species to be comparable, about 44% (Table 2). The combined categories of common and abundant species are used for most other comparisons. Five of the 26 species are common or abundant at both sites: Ceratina acantha Provancher; Habropoda miserabilis Cresson; Bombus occidentalis Greene; Dialictus longicornus (Crawford); and Lasioglossum pavonotum (Cockerell) (Table 3). Andrenidae are common at Bodega, but rare at Arcata dunes, while Megachilidae are prevalent at Arcata dunes and scarce at Bodega. Uniquely abundant species at Bodega include Andrena barbilabris Kirby; Anthophora *bomboides* stanfordiana Cockerell: Melissodes *pallidisignata* Cockerell: and Colletes fulgidus longiplumosus Stephen. Megachile wheeleri Mitchell is uniquely abundant at Arcata dunes. Honey bees, Apis mellifera Linnaeus, are rare at Bodega, but abundant at Arcata dunes due to nearby apiaries and feral populations.

Table 1. Bee faunas of Bodega Marine Reserve (BMR) and Lanphere-Christensen Dunes Preserve (LCDP). Numbers of taxa present and difference $(D)^1$ and resemblance $(R)^2$ of faunas.

Families		Ge	enera				Species	5		
]	BMR	LCDP	Both	D^1	\mathbb{R}^2	BM	R LCDP	Bot	$h D^1$	\mathbb{R}^2
Andrenidae	2	1	1	50.0	50.0	8	4	1	90.9	25.0
Anthophorida	ae 7	4	4	42.9	100.0	12	5	4	69.2	80.0
Apidae	2	3	2	33.3	66.7	8	11	7	41.7	63.7
Colletdae	2	2	2	0.0	100.0	2	3	1 ³	75.0	33.3
Halictidae	6	5	5	16.7	100.0	10	10	6 ³	57.1	60.0
Megachilidae	e 6	5	4	42.9	80.0	7	10	3 ³	78.6	30.0
Totals	25	20	18	33.3	90.0	47	43	22	67.7	51.

 1 D = Difference = number of taxa not shared/sum of taxa x 100

 2 R = Resemblance = number shared taxa /number of taxa in smallest x 100

³ Excluding some undetermined specimens.

Table 2. Relative abundance of bees at Bodega Marine Reseve (BMR) and Lanphere-Christensen Dunes Preserve (LCDP). Based on relative numbers of voucher specimens collected and observations of bee abundance at peak of active season. Ratings: Rare <5; Uncommon 5-10; Occasional 11-25; Common 26-50; Abundant >50. Numbers and percentages of species.

	BMR	LCDP
Rare	14 (29.8%)	13 (30.2%)
Uncommon	7 (14.9%)	6 (14.0%)
Occasional	11 (23.4%)	9 (20.9%)
Common	3 (6.4%)	6 (14.0%)
Abundant	12 (25.5%)	9 (20.9%)
Totals	47	43

Table 3. Bees that are common to abundant¹ at one or both sites: Bodega Marine Reserve (BMR) and Lanphere-Christensen Dunes Preserve (LCDP).

Bees	BMR	LCDP				
Andrenidae						
Andrena (Andrena) saccata Viereck	А	R				
A. (Augandrena) plumiscopa Timberlake	С					
A. (Leucandrena) barbilabris Kirby (=placida Smith)A						
Anthophoridae						
Anthophora bomboides stanfordiana Cockerell	Α					
Ceratina acantha Provancher	Α	С				
Epeolus minimus Robertson	С	0				
Habropoda (=Emphoropsis) miserabilis (Cress	on) A	А				
Melissodes (Eumelissodes) pallidisignata Cock	erell A					
Apidae						
Apis mellifera Linneus	U	А				
Bombus (Bombus) occidentalis Greene	А	А				
B. (Fervidobombus) californicus Smith	R	С				
B. (Pyrobombus) bifarius Cresson	А					
B. (P.) caliginosus (Frison)	0	С				
B. (P.) mixtus Cresson		А				
B. (P.) sitkensis Nylander	R	А				
B. (P.) vosnesenskii Radoszkowski	А	U				
Colletidae						
Colletes fulgidus longiplumosus Stephen	А					
Colletes hyalinus oregonensis Timberlake		С				
Halictidae						
Dialictus cabrilli (Cockerell)	С	U				
D. longicornis (Crawford)	А	А				
Halictus rubicundis (Christ)	А	0				
Lasioglossum pavonotum (Cockerell)	А	А				
Megachilidae						
Anthidium palliventre Cresson	0	А				
Coelioxys (Boreocoeloxys) rufitarsus Smith		С				
Megachile (Xeromegachile) wheeleri Mitchell		А				
Osmia (Acanthosmioides) integra Cresson		С				

¹Abundance scale: $R = \langle 5; U = 5-10; O = 11-25; C = 26-50; A = \rangle 50$.

Most species from both sites exhibit the western North American and Pacific Coast area biogeographic distribution patterns (Table 4). California endemics are most prominent at Bodega.

Table 4. Biogeographic distribution patterns of bee species occurring at Bodega Marine Reserve (BMR) and Lanphere-Christensen Dunes Preserve (LCDP) (excluding undetermined species, mostly Halictidae and Nomadinae). Numbers of species.

	1			
A	11	Common/Abundant		
BMR	LCDP	BMR L	.CDP	
2	1	2	0	
2	6	1	2	
n 16	17	3	7	
10	11	5	4	
8	4	4	1	
2	1	0	1	
40	40	15	15	
	2 2 16 10	10 11	BMR LCDP BMR L 2 1 2 2 6 1 16 17 3 10 11 5 8 4 4 2 1 0	BMR LCDP BMR LCDP 2 1 2 0 2 6 1 2 16 17 3 7 10 11 5 4 8 4 4 1 2 1 0 1

Prior to April bee activity is low, but bumble bee queens and *Lasioglossum pavonotum* are present at both sites along with several species of *Andrena* at Bodega. The peak of bee abundance at both sites is from April through June. Some distinctive elements are added in June (*Melissodes pallidisignata* at Bodega and *Megachile wheeleri* at Arcata dunes), but there is a decline in diversity and abundance in August and September.

The percentage of specialist (oligolectic) bees is greater at Bodega that at Arcata Dunes (19.2% vs. 7.0%). This corresponds with the greater numbers of Andrenidae and Eucerini at Bodega. The pollen preferences of 15 to 23% of the bees at the two sites is unknown, however most of these are predicted to be generalists based on available knowledge of related species.

Most of the bees at the two sites are solitary nesting: 66% at Bodega and 58% at Arcata Dunes. Social bees (Apidae) represent 17% of the Bodega fauna and 21% of the fauna at Arcata Dunes. The degree of sociality of the species of *Dialictus* (4% at each site) is unknown. Cuckoo (cleptoparasitic) bees comprise 17% of the fauna at Bodega and 21% of the fauna at Arcata dunes. *Nomada* spp. which parasitize *Andrena* are unique to Bodega. *Coelioxys rufitarsus* Smith, which parasitizes *Megachile wheeleri*, and *Psithyrus fernalde* Franklin and *P. insularis* (Smith) which parasitize *Bombus* spp. are unique to Arcata dunes.

Nest habitats for about 32% of the bees at both sites were determined. Among the abundant and common bee species: Habropoda nest in open sand in blowout areas in the dunes; and Ceratina excavate nests in pithy stems of Asteraceae at both sites. Most of the Halictidae nests were found in compacted soils: sand and decomposed granite at Bodega, sand and clay (reclaimed mud flats) adjacent to Arcata dunes. Anthidium females nest in areas of established dune vegetation in both areas, especially at the edges of deflation plains. Most of the rest of the bees at Arcata dunes nested in the established dune vegetation: Megachile wheeleri, Osmia integra Cresson, Colletes hyalinus oregonensis Timberlake and Lasioglossum pavonotum. At Bodega, Andrena barbilabris nested in open sand and midden mounds; Melissodes pallidisignata nests in compacted sand such as deflation plains in the dunes and paths near the laboratory; Anthophora bomboides, A. californica Cresson and Colletes fulgidus nest in vertical sandstone cliffs, especially at the end of Horseshoe Cove. Anthophora bomboides is further limited by the need for sources of fresh water for use in excavating its nests in sandstone cliffs.

Habitat types at Bodega include: beach, dunes, cliffs of sandstone or decomposed granite, and grasslands,

with the latter comprising much of the reserve (Barbour *et al.*, 1973). Arcata dunes is a smaller area with beach, dunes, and forest, with dunes making up most of the open area. The dunes at Bodega are not as diverse as those at Arcata. There are some relict dunes with native vegetation, but much is dominated by introduced beach grass with little original flora remaining.

The floras of the two sites show a considerable degree of difference (Table 5). There is a low resemblance of the smaller flora at Arcata dunes with that of Bodega. This pattern is heightened when only the portions of the floras actually visited by bees are compared. Although the overall taxonomic diversity of flowering plants is higher at Bodega, a higher proportion of the flora at Arcata dunes is visited by bees.

Table 5. Floras of Bodega Marine Reserve (BMR) and Lanphere-Christensen Dunes Preserve (LCDP). Comparisons of all¹ flowering plants and bee-visited taxa including numbers and percentage introduced species. Numbers of taxa present and difference $(D)^2$ and resemblance $(R)^3$ of floras.

	All ¹					Bee Visited				
	BMR	LCDP	Both	D^2	\mathbb{R}^3	BMR I	LCDP	Both	D^2	\mathbb{R}^3
Families	37	39	27	55.1	73.0	18	21	12	55.6	66.7
Genera	111	95	62	56.9	65.3	37	45	17	73.9	46.0
Species	156	127	58	74.2	45.7	39	50	15	79.7	38.5
Introduced	54	34	18	74.3	52.9	9	14	5	72.2	55.6
% Intro	34.6	26.8				23.1	28.0			

Angiospermae except: Betulaceae, Cyperaceae, Graminiae, Juncaceae, Juncaginaceae, Lemnaceae, Potamogetonaceae, Sparganiaceae, and Zosteraceae.

² D = Difference = number of taxa not shared/sum of taxa x 100

 3 R = Resemblance = number shared taxa /number of taxa in smallest x 100.

At Arcata dunes, ericaceous shrubs dominate the flora prior to April, but these are not found at Bodega. In April through June, Legumes (*Lathyrus* and *Lupinus*) dominate Arcata dunes, while a greater diversity of flowers occurs in the grasslands at Bodega including: *Amsinkia*, *Armeria*, *Eschscholzia*, *Lasthenia*, *Layia*, *Lupinus*, and *Nemophila*.

July through September is dominated by Asteraceae at both sites.

Flowers that do not produce nectar as a reward are visited primarily by generalist bees that obtain nectar from other plants in the same area (Table 6). This is particularly apparent when bees with bright orange pollen loads from *Lupinus* are seen visiting flowers with lighter-colored pollen such as *Amsinkia*, *Armeria*, or *Stachys*.

Table 6. Flowers and principal bee visitors at Bodega Marine Reserve categorized by types of reward for bees.

Reward and flowers	Dominant bee visitors
Pollen only	
Lupinus arboreus	Bombus, Habropoda
Lupinus spp.	Bombus
Eschscholzia	Bombus, Andrena, Halictidae
Primarily nectar	
Armeria	Andrena, Bombus, Colletes, Halictidae
Stachys	Anthophora, Bombus
Both pollen and necta	r
Amsinkia	Bombus, Habropoda
Potentilla	Andrena, Bombus, Colletes, Halictidae

Different genera of Asteraceae may receive visits from predominantly specialist bees (*Lasthenia*), combinations of specialist and generalist bees (*Layia*, *Erigeron*) or generalist bees (*Eriophyllum*) (Table 7). Introduced flowers are predominantly visited by generalist bees (Table 7). In addition, the few flower visits by honey bees recorded at Bodega were all to flowers of introduced plants: *Myoporum* (5), *Cirsium vulgare* (Savi) Ten. (2), and one each to *Carpobrotus* and *Raphanus*.

Table 7. Selected groups of flowering plants and theirprincipal bee visitors at Bodega Marine Reserve.

Flowering plant taxa Dominant bee visitors					
Asteraceae					
Lasthenia	Andrena				
Layia	Andrena, Colletes, Halictidae				
Erigeron	Bombus, Ceratina, Colletes, Melissodes				
Eriophyllum	Bombus, Halictidae				
Introduced plants					
Carpobrotus	Bombus, Halictidae				
Hypochoeris	Bombus, Ceratina, Colletes, Halictidae				
Myoporum	Bombus, Halictidae				
Raphanus	Anthophora, Habropoda				

Comparative measurements of bee visitation to *Lupinus arboreus* Sims, (1,000 racemes), *Erigeron glaucus* Ker. (200 heads), *Potentilla egedei* Wormsk. (200 flowers), and *Amsinkia menzeisii* (Lehm.) Nels. & Macbr. (1,000 cymes) in June 1991 at Bodega showed low but recordable visits of 1 to 4 bees per minute on all but the *Lupinus* which received no visits. Some bees had been observed visiting the *Lupinus* in April and May. Some fruit was set by June, but there

were distinct gaps where entire whorls of flowers had failed to set seed or aborted on these racemes.

Discussion

Diversity of host-specific bees in California is low (30%) in coastal communities in contrast to other zones, even lower than in alpine areas (Moldenke, 1976a, b). Our figures for Bodega and Arcata show even lower percentages of specialist bees. Therefore plants in these coastal areas are primarily visited by generalist bees. Moldenke (1975) shows that bumble bees increase in abundance with increasing severity of environment, being highest at his coastal site (Point Reyes). Our data show highest diversity and abundance of bumble bees at Arcata corresponding to the findings of Thorp *et al.* (1983).

Estimates of relative abundance of bees were made from collections and observations at flowers and at nest sites. Each may give a different impression of abundance. Large concentrations of bees at aggregated nest sites leave the impression of high abundance if the area of the nests is not put in perspective with the entire study area. Bees may disperse rapidly from the nest site over mass blooming flowers nearby and be diluted quickly giving quite a different impression during the flower visitation counts. Generalist bees may be further diluted by visiting diverse host flowers.

The biogeographic patterns of the bees at the two sites show that they each are derived from a variety of sources. The presence of many of the same species of bees on San Miguel Island, Santa Barbara County, California (Table 8) suggests a strong affinity among the coastal areas from southern Oregon to Point Conception, California. *Dialictus cabrilli* was thought to be endemic to San Miguel Island (Rust *et al.*, 1985), but is now known from Bodega and Arcata dunes. *Bombus nevadensis miguelensis* Cockerell is a dark form of the widespread nominate species from San Miguel Island. The same color form occurs as a disjunct population at Arcata (Thorp *et al.* 1983).

Because most of the bees at the two sites are solitary and ground-nesting, soil substrate is important in determining the composition of the bee communities. Gordon (1992) has also shown that *Megachile wheeleri* nest sites are closely associated with certain plants. The lack of compacted sand and vertical cliffs at Arcata dunes limits nesting of some of the more common species found at Bodega such as *Melissodes pallidisignata*, *Anthophora bomboides*, and *Colletes fulgidus*. The fact that *Melissodes* have been found nesting in compacted sand along roads within five miles of the Arcata dunes (DMG) confirms this limitation.

Table 8. Bees of San Miguel Island, Santa Barbara
County, California (Rust et al., 1985) that also occur
at Bodega Marine Reserve (BMR) and Lanphere-
Christensen Dunes Preserve (LCDP).

Bees	BMR	LCDP
Dialictus cabrilli (Cockerell)	+	+
Bombus nevadensis miguelensis Cocke		
B. californicus Smith	+	+
B. vosnesenskii Radoszkowdki	+	+
Colletes hyalinus Provancher	-	+
Andrena submoesta Viereck	+	-
Andrena caerulea Smith	+	-
Lasioglossum pavonotum (Cockerell)	+	+
Osmia albolateralis Cockerell	+	+
Epeolus minimus Robertson	+	+
Anthophora californica Cresson	+	-
Habropoda miserabilis (Cresson)	+	+

 1 + =present; - =absent.

From the standpoint of flower resources, Tepedino (1979) suggested that generalist bees would be less vulnerable to extinction than specialists. However, floral resource generalists may have specialized requirements for nest sites. Our studies suggest that location of the nest sites of many bees at Bodega and Arcata are determined in large measure by soil type. Thus, they may nest in different habitats from those containing the flowers they pollinate. If the bee nest habitats are not included under the same management goals as those of the flowers, their protection cannot be assured and a vital link in the reproductive biology of the plant communities may be weakened. There is need for further studies of the nesting biology of bees in managed areas because of their importance as pollinators.

Proper identification of biological specimens is of prime importance in any biological diversity study. Many bee taxa are not well known due to the lack of scientists willing to revise large taxa of small sized insects. Thus, many of the Halictidae and parasitic Anthophoridae are difficult to get identified. The initial databases at both sites contained records of individual specimens that were suspicious based on known distributions and sources of the material. These records have been eliminated from consideration here because we have not been able to validate them. The specimens have been retained for further study. We have established voucher collections of identified specimens collected by us with source information for future comparisons.

In developing a database of flower association records for bees, it is important to record the type of visit and resource collected. Bees visiting flowers that produce pollen only may also require brief diversions to nectar producing flowers to maintain their energy supplies for flight. Accumulated records of flower associations of bees occur in monographs (e.g., Moldenke and Neff, 1974) and the Hymenoptera catalog (Krombein, et al. 1979). However, these depend upon the presence and accuracy of flower host labels on museum specimens. Many monographs and catalogs merely provide lists of plant taxa without weighting frequency of encounter. They often lack information as to whether the flower records represent visits for pollen, nectar, both, or may be only incidental associations. Such lists overemphasize diversity of rare occurrences and undervalue common use or possible specialization.

Flower visits by *Apis* at Arcata where it is abundant were not included because of the focus on native bees, but limited records from Bodega are all to introduced flowers. The tendency for Apis to frequent introduced flowers has been noted by Donovan (1980) in New Zealand and other study sites in California (RWT). Thus, *Apis* may be of limited value in maintaining populations of native plants in areas of its introduction.

Introduced flowering plants may affect flowering plant communities in a number of ways. They may crowd out native plants in competition for space, cover bee nest sites, compete with natives for services of pollinators, enhance reproduction of alien bees which may in turn compete with native bees, and provide additional sources of pollen and nectar for native bees, especially generalists. These diverse roles should be evaluated before management actions are initiated.

The low relative abundance of bees at Bodega, especially during the summer months when weather (e.g., fog, wind, cold) limits pollinator flight suggests that many of the plants may be pollinator limited. Quantitative measures of bee visitation to patches of flowers show low abundance of bees relative to bloom abundance even during the best of weather at Bodega. There are also striking differences in visitation to different plants supporting the same pollinators (e.g. Lupinus arboreus versus Amsinkia menziesii). Pollen limitation is further supported by observations of gaps in fruit production in racemes of Lupinus arboreus. This is of particular interest since Lupinus arboreus may be a keystone species in the grasslands at Bodega. By contract, it is considered a weed in the dunes at Arcata (Miller, 1988). Studies of its reproductive biology at both sites should be of considerable importance.

In conclusion, there are many differences and similarities in the two managed coastal habitats

examined here. The composition and abundance of the bee faunas are determined by a variety of conditions including soil, climate, plant community, and biogeographic history. A similar pattern at both sites is the frequent separation of habitats required by bees for nesting and for food foraging. We are beginning to see evidence that broad applications of pesticides in forests to control spruce bud worm (Kevan and LaBerge, 1978; Plowright et al., 1978) depresses crop pollinator populations. Similarly, rangeland sprays to control grasshoppers are threatening pollinators of endangered plant species (Tepedino et al. 1990). Grazing and trampling of nest sites may also adversely effect pollinators of endangered plant species (Sugden, 1985). For continued reproductive success of many of the elements of the plant community, conservation biologists must consider protecting additional habitats needed by their pollinators. This has been anticipated by Frankie et al. (1990) who suggest the need to evaluate habitats near preserve because they "may function as important reservoirs of target pollinator groups." Our studies also indicate that there is a need to conserve mosaics of habitats, especially where large generalist bees are important as long-range pollinators.

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