DOI: 10.1007/s002679910035

ENVIRONMENTAL AUDITING

Arthropod Monitoring for Fine-Scale Habitat Analysis: A Case Study of the El Segundo Sand Dunes

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ABSTRACT / Arthropod communities from several habitats on and adjacent to the El Segundo dunes (Los Angeles County, CA) were sampled using pitfall and yellow pan traps to evaluate their possible use as indicators of restoration success. Communities were ordinated and clustered using correspondence analysis, detrended correspondence analysis, two-way indicator species analysis, and Ward's method of agglomerative clustering. The results showed high repeatability among replicates within any sampling arena that permits discrimination of (1) degraded and relatively undisturbed habitat, (2) different dune habitat types, and (3) annual change. Canonical correspondence analysis showed a significant effect of disturbance history on community composition that explained 5–20% of the variation. Replicates of pitfall and yellow pan traps on single sites clustered together reliably when species abundance was considered, whereas clusters using only species incidence did not group replicates as consistently. The broad taxonomic approach seems appropriate for habitat evaluation and monitoring of restoration projects as an alternative to assessments geared to single species or even single families.

Although researchers have documented the numerical preponderance of arthropods within terrestrial communities (Gaston 1991), their use in monitoring for purposes of conservation biology has been limited (Kremen and others 1993) but is increasing (Parmenter and MacMahon 1990, Parmenter and others 1991, Niemelä and others 1993, Williams 1993, Garono and Kooser 1994, Streever and others 1996, Andersen 1997, Andersen and Sparling 1997, Rykken and others 1997, Lawton and others 1998). Their role in ecosystem function is significant across all levels of food chains, from herbivores to detritivores to parasitoids, prompting Wilson (1987) to refer to them by his oft-quoted remark as "the little things that run the world." An especially important attribute of these animals lies in their microgeographic distributions, which may reflect fine-scale heterogeneity in habitats to which most vertebrates are insensitive.

With the growing trend of attempting restoration of degraded habitats, monitoring the dynamics of arthropod assemblages may provide the most convincing evidence for estimating success or failure of any given project. Because of high turnover and growth rates for most species, arthropods serve as probes that quickly respond to environmental change. They are also assayed inexpensively and efficiently with a few simple trapping methods. Our paper presents a 3-year study to assess arthropod assemblages on habitats having experienced different degrees of disturbance on the El Segundo sand dunes in coastal Los Angeles County, California. Our intention is to develop a method to evaluate revegetation attempts on the dunes. The results show high repeatability among replicates within any sampling arena that permits discrimination of (1) degraded and relatively undisturbed habitat, (2) different habitat types, and (3) annual change.

The El Segundo sand dunes persist as a 115-ha fragment of their former 1200-ha extent, bordered by the Pacific Ocean to the west and historically surrounded by the Los Angeles coastal prairie (Mattoni 1993, Mattoni and Longcore 1997). Dense urban development isolates the surviving habitat. Persistence of the fragment depends on its location at the west end of the Los Angeles International airport (LAX). Prior to construction of the present airport configuration, developers had built 850 homes on part of the land, including some still under construction when a referendum permitted condemnation and removal of the residences in the 1970s. The residential development and construction of a major highway that now borders the east side of the fragment reduced relatively undisturbed dune habi-

KEY WORDS: Arthropods; Ecological monitoring; Revegetation; Restoration; Correspondence analysis; Canonical correspondence analysis; Cluster analysis

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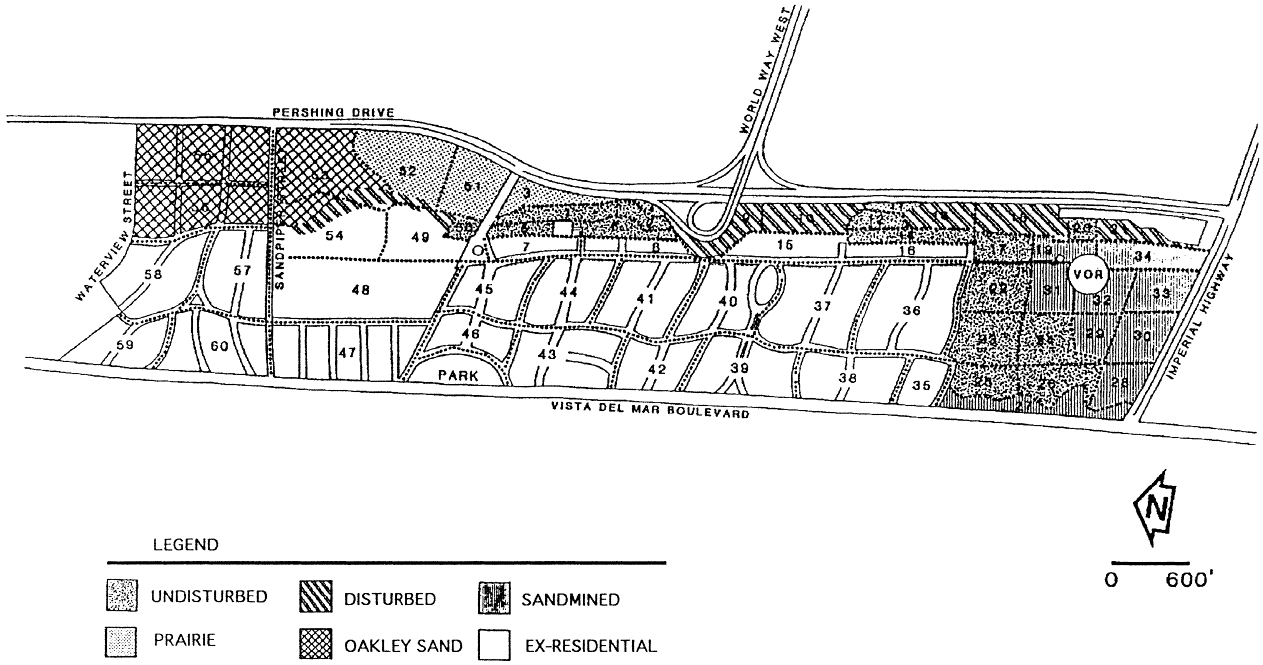

Figure 1. Map of site designations on the El Segundo dunes at the Los Angeles International Airport with a superimposed classification of habitat types based on historic land disturbance.

tat to 16 ha. The authority of the Endangered Species Act, invoked to protect the endangered El Segundo blue butterfly, *Euphilotes bernardino allyni,* in combination with political action engendered by active environmental groups, led to 80 ha of the 120-ha parcel owned by the airport to be set aside as a preserve in 1991. The only surviving fragment of the coastal prairie is a totally degraded 10 ha within the preserve area, a fraction of its historic 95 km^2 extent.

We classify habitats across the preserve as ex-residential, sandmined, and undisturbed foredune, disturbed and undisturbed backdune, and disturbed prairie and Oakley sand, as they existed prior to commencement of the revegetation effort in 1989 (Figure 1). Edaphic characteristics define the two major habitats, dunes and prairie. Free-flowing sand characterizes the dunes, and the consolidated sand of a Pleistocene dune formation underlies the prairie (Cooper 1967). A third edaphic area of Oakley sand occupies 10 ha at the NE corner of the airport land and is presently outside the preserve limit (Nelson 1919). The Oakley sand appears to be a result of intensive earlier farming practice, which we classify as prairie substrate, that farmers repeatedly ploughed and fertilized. The dunes proper are sharply differentiated into foredune and backdune, the foredune formed by the gradual upslope of sand from the strand, the backdune by the unstable slope of sand eroding from the dune crest (Cooper 1967). The topoclimatic effect of the two aspects correlates with floral communities differing in amount of cover and species composition. The foredune, in contrast with the backdune, is subject to almost continuous diurnal westerly winds and drying afternoon sun. During the warmest summer months, the backdune usually escapes morning solar exposure because of fog. These factors, combined with wind deflection, make the backdune on average more humid with ameliorated temperatures.

Degradation of the site involved three activities: (1) home construction with import of foreign soil to aid landscaping, (2) road building with attendant grading, and (3) sandmining for contouring the radar hill or VOR (Figure 1). Removal of the residences in the 1970s was superficial, leaving some foundations, substantial rubble, foreign soil, roads, and other infrastructure. Vegetation regenerated without assistance, producing a cover of predominately iceplant (*Carpobrotus edulis*) and acacia (*Acacia cyclopis*) with patches of a few highly dispersive dune shrub species. Contouring the backdune for road construction was more destructive. An airport contractor revegetated the contoured slopes in 1975 with a "native" seed mix of coastal sage species, none of which was native to the dunes (including *Eriogonum fasciculatum, E. giganteum, E. cinereum, Coreopsis gigantea, Atriplex canescens, Lupinus excubitus,* and other non-native species). The landscaper also applied the same mix to the entire prairie area. The only species of this mix to persist was the California buckwheat (*E. fasciculatum*), the cover otherwise becoming again chiefly iceplant and acacia. This alien buckwheat was an important factor threatening the viability of the small population of the El Segundo blue butterfly then present by bolstering populations of competing Lepidoptera (Pratt 1987). The sandmined area revegetated naturally. The flora that reestablished there, although covered with high density of iceplant and acacia, carried a 50% higher cover of dispersive native shrubs than the ex-residential area, probably a consequence of clean sand being exposed without a human artifact load with all edges bordering undisturbed sites (Figure 1). Mattoni directed efforts in 1986–1989 to remove the exotic buckwheat, iceplant, and acacia across undisturbed dune sites, followed by a revegetation project completed in 1994. However, none of the areas used in this study were revegetated during the study period.

Methods

We quantified arthropod assemblages using two monitoring methods: pitfall and yellow pan traps. Pitfall trapping samples a large variety of ground dwelling species, mostly arachnids, ametabolous insects, Coleoptera, and Diptera. Although several biases in both randomness of sampling and absolute correlation to densities of specific taxa are inherent in the method (Southwood 1966, Baars 1979, Spence and Niemalä 1994), the technique is powerful for comparative purposes of habitat evaluation by sampling a large number of diverse taxa. Baars (1979) presented evidence that pitfall trapping provided an accurate estimate of population size for carabid beetles. Although correlative information is not available for other groups sampled, we believe the technique is valid for purposes of intercommunity evaluation of all taxa sampled given standard conditions of application. We have recorded 189 species from pitfall traps across the dunes and prairie.

Yellow pan traps capture flying species attracted to yellow colored flowers. This assemblage generally includes insects that are vagile flower herbivores, pollinators, predators, and associated parasitoids. Most are Hymenoptera, Diptera, and Coleoptera. Despite possible objections to the limiting values of this methodology, our findings indicate the technique is repeatable in sampling a large and diverse set of taxa. We have collected 169 species in yellow pan traps.

Pitfall traps consist of two 1-quart plastic containers, each 10 cm across and 13 cm deep, nested together and buried so that the rim of the inner container was flush with the sand. Nesting facilitates trap removal of the inner container without requiring repositioning of the traps in caved-in sand each time the trap is taken up to remove its contents. We smoothed the sand surface to the rim and covered it with a 20-cm square thin plywood lid supported 2 cm above the rim by wooden legs. We filled the traps to a depth of 2 cm with ethylene glycol as preservative and collected the contents at 2- to 3-week intervals, depending on climatic conditions. We collected all sample stations on the same day.

Yellow pan traps were 1-pint plastic containers painted lemon yellow. We filled them with 2 cm of ethylene glycol and generally placed them adjacent to the pitfall traps, but buried about 2 cm in the sand to minimize loss during heavy winds. Collection was always concordant with pitfall sampling. Within 1 day we sorted the contents collected from both trapping methods, scored the readily determinable species using standard keys (Borror and White 1970, White 1983, Borror and others 1989, Arnett 1993), and stored the remainder in 80% ETOH for later determination. We identified many taxa to morphospecies (see Oliver and Beattie 1996a, 1996b) when further identification required expert assistance. We archived all but commonplace species and assembled a reference collection of all species.

We treat two sets of samples here. We (Mattoni 1989) collected the first set as part of an extensive biota survey of the entire airport dunes property in 1988–1989. We arbitrarily divided the property into 60 sites, which varied from 0.2 to 2.5 ha and showed a relatively uniform plant cover and land use history. We classified the sites as follows: undisturbed backdune (5 sites), undisturbed foredune (8), disturbed backdune (5), disturbed foredune (25), sandmined foredune (9), prairie (5), and Oakley sand (3). We placed a single pitfall trap within each of the 60 sites for the 1988–89 survey and sampled as described above. Concurrently, we conducted a botanical survey to record higher plant species for each site. The survey included native, nonnative, and persistent ornamental plants with mapping of iceplant cover and acacia distribution.

We collected the second set of data in 1992–1993, when we placed replicate sets of three or four pitfall traps within selected sites. We further sampled some sites with triplicate yellow pan traps. Trap placement configurations both varied from linear to staggered, but in all cases were spaced at 5-m intervals. The stations sampled by pitfalls and yellow pans represented undisturbed backdune (site 20), undisturbed foredune (site 22, sampling started in 1993), disturbed foredune (site 36), and Oakley sand (site 51). Stations sampled by pitfall traps only included prairie (site 3, traps 1–4 placed 10 m from the backdune slope toe, traps 5–8 placed 10 m from the east boundary, the two sets separated by about 100 m) and disturbed foredune (site 19). Yellow pan traps alone sampled one undisturbed backdune location (site 1).

Table 1. TWINSPAN analysis of vegetation surveys and samples from pitfall traps and yellow pans. Groups of samples produced by the first two TWINSPAN divisions in each data set (one in yellow pans) are depicted, and the number of samples from different habitats in each such group is given

	Vegetation			Pitfalls 1988				Pitfalls 1992–93			Pans 1992–93	
Ex-residential foredune	1	2	21	2	9	9	4	0	0	7	0	9
Sandmined foredune	0	3	6	0	9	0	0	0	0	6	NA	
Undisturbed foredune	0	7	1	0	9	0	0	0	4	0	3	0
Disturbed backdune	1	0	4	2	3	0	0		NA		NA	
Undisturbed backdune	0	5	0	4	1	0	0	0	0	7	12	0
Prairie	3	0	2	2	0	0	3	10	1	0	1	2
Oakley sand	3	0	0	0	0	0	3		NA		NA	

Table 2. Cluster analysis (Ward's method, relative Euclidean distance) of samples from pitfall traps and yellow pans. Major groups of samples produced by clustering, and the number of samples from different habitats in each such group are given

	Pitfalls 1988			Pitfalls 1992–93			Pans 1992–93		
Ex-residential foredune	1	10	13	0	7	0	0	3	6
Sandmined foredune	8	1	0	0	0	6		NA	
Undisturbed foredune	6	3	0	0	0	4	0	3	0
Disturbed backdune	2	3	0		NA			NA	
Undisturbed backdune	1	4	0	0	0	7	9	3	0
Prairie	0	2	3	11	0	0	0	3	0
Oakley sand	0	0	3		NA			NA	

Cluster and ordination methods established relationships between sample composition and both habitat type and disturbance history. Many textbooks (e.g., Gauch 1982, Legendre and Legendre 1983) provide technical descriptions of methods used here, so they are not discussed further. TWINSPAN, a divisive clustering method, grouped samples based on species composition without regard to species abundance. Ward's method of agglomerative clustering based on relative Euclidean distance grouped samples using species abundance. Quantitative data were also analyzed by correspondence analysis (CA) with detrending (DCA) applied whenever a "horseshoe effect" in the results was detected. Abundance data were log $(n + 1)$ transformed prior to analyses. These analyses order samples according to the similarities in their composition, using no explicit information on environmental variables associated with the samples.

We tested the response of arthropod communities to disturbance with canonical correspondence analysis (CCA). This direct ordination method relates the composition of samples to external (environmental) variables. The method permits testing significance of the relationships between external variables and sample composition and estimates the percentage of variability in the species composition data attributable to these variables (ter Braak 1986, ter Braak 1987–1992, ter Braak and Prentice 1988). We constrained the canonical ordination with historical disturbance intensity to determine the degree to which it explained variability in the composition of the samples. We assigned values of disturbance intensity as: 2 for ex-residential plots, 1 for sandmined and recontoured dunes, and 0 for undisturbed dunes.

Results

TWINSPAN analysis of the species composition of native plants in our 60 plots (Table 1) separated nondune and dune habitats in the first step; the algorithm thereafter divided dune samples into two groups according to their disturbance level. Analyses based on arthropod species composition of samples collected by pitfalls and yellow pans are consistent with this pattern. In pitfall data from 1988, undisturbed backdune, sandmined and undisturbed foredune, ex-residential foredune, and nondune habitats dominated the four groups of samples produced by clustering. In pitfall data from 1992 and 1993, the analysis separated nondune and dune habitats, but further division of dune habitats was not consistent with differences in their disturbance level. The separation of the yellow pan samples into two groups reflected accurately different disturbance intensities to which they had been exposed. Cluster analysis, based on quantitative data, show a consistent pattern for all three analyses (Table 2). Samples from nondune habitats, and those from highly disturbed ex-residential foredune, tend to form clusters separate from other samples.

Cluster analysis detected strong effect of local conditions on sample composition, too. Each year, nine sites

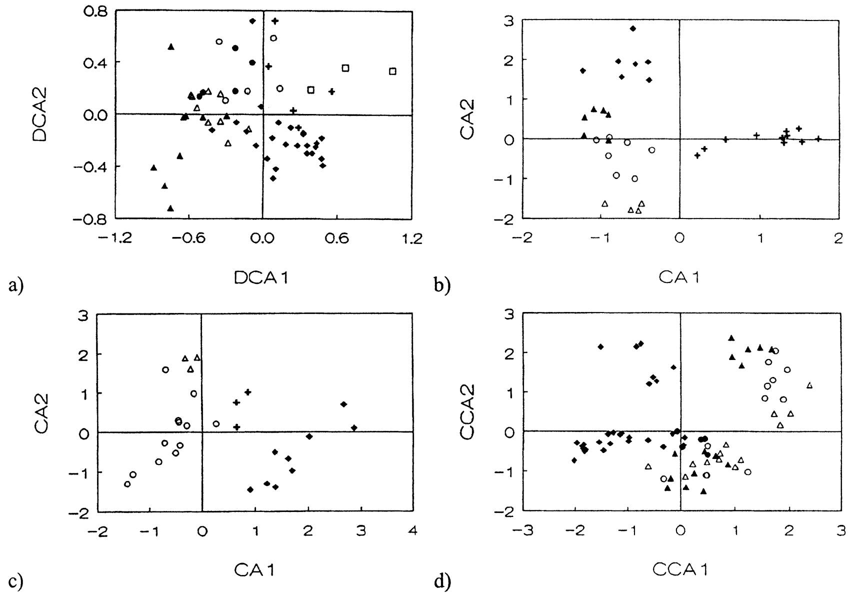

Figure 2. Markers denote different habitat types: ◆ ex-residential foredune, ▲ sandmined foredune, △ undisturbed foredune, ● disturbed backdune, ○ undisturbed backdune, + prairie, □ Oakley sand. a) DCA ordination of pitfall trap samples from 1988; b) CA ordination of pitfall trap samples from 1992 and 1993; c) CA ordination of yellow pan samples from 1992 and 1993; d) CCA ordination of pitfall trap samples from 1988, 1992, and 1993 with disturbance intensity as the external constraining variable.

had three yellow pans each; similarly, in pitfall trap sampling program, nine sites had eight, four, four, four, three, three, three, three, and three replicated traps. In cluster analysis, seven out of nine of these sets of replicated traps were put together, forming a single exclusive cluster in each case. We obtained this result with both yellow pans and pitfalls, indicating that our sampling was highly repeatable and that the samples from the same plot and year represented coherent groups. High repeatability of sampling results is less obvious when only species composition, not species abundance, is analyzed. Thus, with TWINSPAN analysis only four out of nine groups of replicated yellow pans were clustered together and only two of seven such groups of pitfall traps.

Indirect ordination analyses also show a distinct effect on the sample composition of the habitat type. It is detectable, although not very clear, in the pitfall data from 1988 (Figure 2a); samples from pitfall and yellow pan trapping from 1992 (Figure 2b) and 1993 (Figure 2c) all grouped in a close correspondence with the habitat to which they belonged. Nondune and highly disturbed ex-residential habitats were separated from the rest of the data.

We tested the effect of habitat disturbance on the composition of samples in dune habitats with CCA ordinations (Table 3, Figure 2d). Historical disturbance intensity explained a significant amount of variation in the composition of samples in both foredune and backdune habitats: $P = 0.03$ (Monte Carlo method, 999 random permutations) for pitfalls in backdune samples, and $P = 0.001$ for both pitfalls and yellow pans in foredune samples. Disturbance intensity is closely correlated with the first, canonical, axis ($r > 0.8$ in all analyses). As it is obvious from the comparison of canonical and unconstrained eigenvalues, the percentage of variance in sample composition explained by disturbance as an environmental factor is rather low (5–20%). We attribute this, at least in part, to differences in the sample composition between years. In the CCA analysis of pitfall samples from all dune habitats and years (Figure 2d), the spread of the samples along the second axis reflects residual variability in their composition not attributable to the gradient in disturbance intensity. A strong effect of between-year variability is apparent as samples are ordered along the second axis according to the year of the study; all samples from 1988 have negative scores on this axis, but all samples from 1992 and 1993 have positive ones.

Table 3. CCA ordination of pitfall trap and yellow pan samples with the disturbance intensity as an external (environmental) variable. Pitfall samples from 1988, 1992, and 1993, and yellow pan samples from 1992 and 1993 were used

	Backdune pitfalls	Foredune pitfalls	Foredune yellow pans
Eigenvalue X1 (constrained)	0.130	0.111	0.433
Eigenvalue X2 (unconstrained)	0.216	0.160	0.313
Species × Env. correlation, X1	0.926	0.832	0.994
% variance explained, X1	8.6	5.3	20.2
% variance explained, X2	14.3	7.6	14.7
Sum of unconstrained eigenvalues	1.514	2.112	2.137
Sum of canonical eigenvalues	0.130	0.111	0.443
P	0.033	0.001	0.001

Discussion

The results confirm that arthropod communities differ among the different habitats found on the dune system, and that community structure reflects disturbance history. Our effort differs substantially from other uses of arthropods as bioindicators. Historically, scientists have used arthropods to evaluate the effects of environmental pollutants rather than land use history (Rosenberg and others 1986). Efforts to evaluate habitats have usually been limited to specific taxonomic groups (Samways 1990b, Niemelä and others 1993, Pollet and Grootaert 1996, Rykken and others 1997). Though limited taxonomic groups can distinguish habitat differences in some instances, they can also be limiting. Niemelä and others (1993) showed significant differences among ground beetle fauna from boreal forest sites at different times since clear-cutting. Rykken and others (1997) were not able to distinguish ecological land types using ground beetles, but did discover responses to site moisture. In a comparison of created and natural wetlands using common dipteran larvae, Streever and others (1996) were unable to distinguish between the two classes. Our broad taxonomic approach ensures ample variation to distinguish among habitat type and disturbance history. This approach gains support from results surveying tropical forest diversity along a disturbance gradient. Lawton and others (1998) measured eight diverse taxonomic groups (birds, butterflies, flying beetles, canopy beetles, canopy ants, leaf-litter ants, termites, and soil nematodes) and detected an overall decrease in diversity with increased disturbance. However, no one group served as a good indicator for the effects on other groups, establishing the need to sample diverse taxonomic groups to accurately perceive the effects of disturbance.

Our use of multivariate ordination methods to analyze arthropod communities joins a growing number of similar applications (Samways 1990a, Niemelä and others 1993, Garono and Kooser 1994, Pollet and Grootaert 1996, Streever and others 1996, Rykken and others 1997). Similar to results found by Streever and others (1996) for dipteran larvae, the dunes arthropod communities were at best weakly related to environmental variables using CCA. Nevertheless, the degree of discrimination evident in correspondence analysis suggests that the method could be used to track the recovery of arthropod communities following revegetation. The yearly variation shown in the data reaffirms the general tenet that such attempts should compare revegetated and natural reference sites for the same year (White and Walker 1997). With this caveat, we believe that the current method should provide an efficient method to track the success of revegetation efforts undertaken on the dunes. Such an effort is currently under way. In addition, the high correlation between replicates of traps at a single location provides important guidelines for future monitoring using this methodology. Such replication suggests that three traps are sufficient to describe local arthropod community conditions, but only if measures include species abundance.

The ability to distinguish among different land use histories is important to future efforts to monitor the performance of ecological restoration using this method. Whether revegetated sites move closer to undisturbed sites over time will provide a test of restoration performance. The data show that highly disturbed sites do not spontaneously recover over time. Ex-residential foredune is clearly distinguished from undisturbed foredune after 20 years. Sandmined foredune, left to recover without the added impediment of an exotic plant load, is more similar in arthropod community structure to undisturbed foredune, but still shows a measurable difference. While this may be an observation of the obvious, it highlights the need for revegetation in the management of disturbed lands. The establishment of the dune preserve was only the first step in protecting the long-term natural quality of the remaining dunes land. Intensive planting across disturbed foredune and backdune habitats was undertaken in 1993 and 1994 using combinations of native shrubs in patterns to emulate floral densities quantified from undisturbed areas.

We suggest that arthropod monitoring as described here will provide a useful tool to evaluate the restoration attempted on the El Segundo dunes. The method is easily adaptable to other terrestrial habitats, as has been shown by the successful use of arthropod indicators to show environmental recovery in boreal forests (Niemelä and others 1993), tropical forests (Jansen 1997), riparian woodlands (Williams 1993), and scrublands (Parmenter and MacMahon 1987, 1990, Parmenter and others 1991). Use of a community measure to track habitat changes is important to avoid concentration on single species in management and restoration of natural habitats. On the El Segundo dunes the tendency for regulators is to fixate on the El Segundo blue butterfly because of its importance as a federally endangered species. However, 10 other arthropod species are known only from the dunes and their continued persistence depends on management of habitat values beyond those required by the El Segundo blue butterfly. The butterfly depends on a single plant (*Eriogonum parvifolium*), whereas habitat requirements for the other endemic species are largely unknown but certainly broader

Table 4. Arthropod species endemic to the El Segundo dunes

Common name	Scientific name	Specific habitat needs	Status
El Segundo crab spider	*Ebo* new species	*Eriogonum, Haplopappus*	Abundant
El Segundo goat moth	*Comadia intrusa*	*Lupinus chamissonis*	Holding
Ford's sand dune moth	*Psammobotys fordi*	Adults nectar at *Gnaphalium*	Extinct?
El Segundo scythrid moth	*Scythris* new species 1	Generalist	Abundant
Lesser dunes scythrid moth	*Scythris* new species 2	Generalist	Rare
El Segundo Jerusalem cricket	*Stenopelmatus* new species	Unknown	Decreasing?
Dorothy's El Segundo Dune weevil	*Trigonoscuta dorothea dorothea*	*Lupinus*?	Very common
Lange's El Segundo Dune weevil	*Onychobaris langei*	Unknown	Very rare
No common name weevil	*Cylindrocopturus* new species	Unknown	Rare

(Table 4). Arthropod community structure provides an alternative metric to butterfly abundance on the success of management in conserving biodiversity.

Literature Cited

Andersen, A. N. 1997. Using ants as bioindicators: multiscale issues in ant community ecology. *Conservation Ecology* (online) 1:8.

Andersen, A. N., and G. P. Sparling. 1997. Ants as indicators of restoration success: relationship with soil microbial biomass in the Australian seasonal tropics. *Restoration Ecology* 5: 109–114.

Arnett, R. H., Jr. 1993. American insects. Sandhill Crane Press, Gainesville, FL, 850 pp.

Baars, M. A. 1979. Catches in pitfall traps in relation to mean densities of Carabid beetles. *Oecologia* 41:25–46.

Borror, D. J., and R. E. White. 1970. A field guide to the insects: America north of Mexico. Vol. 19, The Peterson field guide series. Houghton Mifflin, Boston, MA, 404 pp.

Borror, D. J., C. A. Triplehorn, and N. F. Johnson. 1989. An introduction to the study of insects, 6th ed. Saunders College Publishing, New York, NY, 875 pp.

Cooper, W. S. 1967. Coastal dunes of California. Vol. 104, Geological Society of America Memoir, Geological Society of America, Boulder, CO.

Garono, R. J., and J. G. Kooser. 1994. Ordination of wetland insect populations: evaluation of a potential mitigation monitoring tool. Pages 506–516. *In* W. J. Mitsch (ed.), Global wetlands: old world and new. Elsevier Science Ltd., Amsterdam.

Gaston, K. J. 1991. The magnitude of global insect species richness. *Conservation Biology* 5:283–296.

Gauch, H. G. 1982. Multivariate methods in community ecology. Cambridge University Press, New York, NY, 298 pp.

Jansen, A. 1997. Terrestrial invertebrate community structure as an indicator of the success of a tropical rainforest restoration project. *Restoration Ecology* 5:115–124.

Kremen, C., R. K. Colwell, T. L. Erwin, D. D. Murphy, R. F. Noss, and M. A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7:796–808.

Lawton, J. H., D. E. Bignell, B. Bolton, G. F. Bloemers, P. Eggleton, P. M. Hammond, M. Hodda, R. D. Holt, T. B. Larsen, N. A. Mawdsley, N. E. Stork, D. S. Srivastava, and A. D. Watt. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* (London) 391:72–76.

Legendre, L., and P. Legendre. 1983. Numerical ecology. Vol. 3, Developments in environmental modelling. Elsevier Science Ltd., Amsterdam, 419 pp.

Mattoni, R. 1989. Species diversity and habitat evaluation across the El Segundo sand dunes at LAX. Los Angeles Department of Airports, Los Angeles, CA.

Mattoni, R. 1993. Natural and restorable fragments of the former El Segundo sand dunes ecosystem. Pages 289–294. *In* J. Keeley (ed.), Interface between ecology and land development in California. Southern California Academy of Sciences, Los Angeles, CA.

Mattoni, R., and T. R. Longcore. 1997. The Los Angeles coastal prairie, a vanished community. *Crossosoma* 23(2):71–102.

Nelson, J. W. 1919. Soil survey of the Los Angeles area, California. US Department of Agriculture, Bureau of Soils, Washington, DC, 77 pp.

Niemelä, J., D. Langor, and J. R. Spence. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conservation Biology* 7:551–561.

Oliver, I., and A. J. Beattie. 1996a. Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecological Applications* 6:594–607.

Oliver, I., and A. J. Beattie. 1996b. Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology* 10:99–109.

Parmenter, R. R., and J. A. MacMahon. 1987. Early successional patterns of arthropod recolonization on reclaimed strip mines in southwestern Wyoming: the ground-dwelling beetle fauna (Coleoptera). *Environmental Entomology* 16: 168–177.

Parmenter, R. R., and J. A. MacMahon. 1990. Faunal community development on disturbed lands: an indicator of reclamation success. Pages 73–89. *In* J. C. Chambers and G. L. Wade (eds.), Evaluating reclamation success: the ecological consideration. USDA, Forest Service, Northeastern Forest Station, Radnor, PA.

Parmenter, R. R., J. A. MacMahon, and C. A. B. Gilbert. 1991. Early successional patterns of arthropod recolonization on reclaimed Wyoming strip mines: the grasshoppers (Orthoptera: Acrididae) and allied faunas (Orthoptera: Gryllacridiidae, Tettigoniidae). *Environmental Entomology* 20:135–142.

Pollet, M., and P. Grootaert. 1996. An estimation of the natural value of dune habitats using Empidoidea (Diptera). *Biodiversity and Conservation* 5:859–880.

Pratt, G. F. 1987. Competition as a controlling factor of *Euphilotes battoides allyni* larval abundance (Lepidoptera: Lycaenidae). *Atala* 15:1–9.

Rosenberg, D. M., H. V. Danks, and D. M. Luhmkuhl. 1986. Importance of insects in environmental impact assessment. *Environmental Management* 10:773–783.

Rykken, J. J., D. E. Capen, and S. P. Mahabir. 1997. Ground beetles as indicators of land type diversity in the green mountains of Vermont. *Conservation Biology* 11:522–530.

Samways, M. J. 1990a. Insect conservation biology. Chapman and Hall, London, 358 pp.

Samways, M. J. 1990b. Species temporal variability: epigaeic ant assemblages and management for abundance and scarcity. *Oecologia* 84:482–490.

Southwood, T. R. E. 1966. Ecological methods with particular reference to the study of insect populations, 2d ed. Chapman and Hall, London, 524 pp.

Spence, J. R., and J. K. Niemalä. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *The Canadian Entomologist* 126:881–894.

Streever, W. J., K. M. Portier, and T. L. Crisman. 1996. A comparison of dipterans from ten created and ten natural wetlands. *Wetlands* 16:416–428.

ter Braak, C. F. J. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167–1179.

ter Braak, C. J. F. 1987–1992. Canoco—a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis 2.1. Microcomputer Power, Ithaca, NY.

ter Braak, C. J. F., and I. Prentice. 1988. A theory of gradient analysis. *Advances in Ecological Research* 18:271–317.

White, P. S., and J. L. Walker. 1997. Approximating nature's variation: selecting and using reference information in restoration ecology. *Restoration Ecology* 5:338–349.

White, R. E. 1983. A field guide to the beetles of North America. Vol. 29, The Peterson field guide series, Houghton Mifflin, Boston, MA, 368 pp.

Williams, K. S. 1993. Use of terrestrial arthropods to evaluate restored riparian woodlands. *Restoration Ecology* 1:107–116.

Wilson, E. O. 1987. The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology* 1:344–346.