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Maintenance of ladybeetle diversity across a heterogeneous African agricultural/savanna land mosaic

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Abstract. The importance of agricultural land for maintaining indigenous biodiversity is an important contemporary issue. A large agricultural estate in Swaziland, which is a mosaic of citrus orchards, exotic tree windbreaks, indigenous riparian vegetation and savanna was investigated. The distribution of larval and adult coccinellids within the habitat types, and the relative influences of temperature, relative humidity, ground insolation and prey presence was assessed over a 2-year period. The highest coccinellid densities and species richness occurred within the orchards. Riparian habitats on the boundaries of the estate were closer to the orchard habitat in species composition than was the natural savanna. Not surprisingly, the presence/absence of prey was the most important variable which determined coccinellid distribution and density in the agricultural landscape. Relative humidity, temperature and ground insolation had no significant effect on coccinellid densities. Some species, such as the exotic *Cheilomenes lunata*, and the indigenous *Scynmus* sp. and *Nephus* sp. were widely dispersed and occurred in all habitats, while the economically important but exotic species, *Rodolia cardinalis* was only within the citrus orchards. Overall, the coccinellid assemblage was not a good indicator of habitat type. Nevertheless, a variety of habitat types (i.e. a heterogenous landscape) appear to be essential for the survival of most coccinellids. Indeed, the heterogeneous agricultural and natural land mosaic provides maximum plant diversity and hence coccinellid diversity, thus increasing the potential for natural control of pest prey species in the orchards, while at the same time maximizing survival of indigenous coccinellids.

Key words: agricultural landscape, citrus, Coccinellidae, diversity, land mosaics

Introduction

With increasing agriculture, natural areas have been fragmented, creating a mosaic of different habitat patches (Gilpin et al. 1992; Fry 1995) with varying suitability for the organisms occurring within the patches. Agricultural areas are usually considered as areas of local natural habitat loss with depauperate biodiversity (Myers 1988), including the African savanna (Scholtz and Chown 1993). Crop fields in particular may be considered as habitat sinks for many species, although beneficial for a few pestiferous ones. In terms of pest control, there is then focus on the surrounding borders as conservation islands or headlands harbouring predators of hosts within the agricultural patch.

It is important not to dismiss the agricultural mosaic as devoid of significant natural biodiversity. The agricultural landscape can, in certain circumstances, be a major supporter of rich biodiversity, at least at the species level (Pimentel et al. 1992; Ryszkowski et al. 1993). In the case of carabid beetles, 25% of European species are confined to arable fields (Murdoch et al. 1972; Booij and Noorlander 1992), while African macadamia orchards have high species richness (Jaganyi 1998).

In agricultural ecosystems, juvenile and adult coccinellids are important predators of pest arthropods, while in natural systems, they regulate ecosystem processes through their suppression of otherwise highly abundant herbivores. It is well-known that they regularly shuttle around the landscape mosaic to locate prey and to oviposit (Hattingh and Samways 1995; Mills 1982; Samways 1984).

Occurrence of coccinellids in specific habitats appears to be controlled by various and varying factors, including prey density and abiotic conditions (Hodek 1973; Majerus 1994) but still little is known of the relative importance of these factors. This is important, as these factors are determinants of local species diversity and abundances. But the question is whether it matters that the vegetation is indigenous or whether it is exotic and agricultural. This, in turn, may determine the extent to which a major landscape feature (i.e. a citrus estate) is a reservoir or a sink for a portion (i.e. coccinellids) of biodiversity. This study aims to ascertain the relative roles of natural versus exotic vegetation for maintaining coccinellid diversity.

Sampling area and methods

The focal area was Tambuti Citrus Estate, Swaziland (26°43′ S–31°43′ E), which has 932 ha under citrus, between and around which is natural savanna (Figure 1). Two sets of four citrus orchards were selected, one set running north–south and the other running east–west. These orchards together also constituted the first of six transects. The next four transects were transition habitats between the orchards and the indigenous natural savanna. In the northern and eastern directions, transects extended up to 400 m into the natural savanna. In the south, the transect was short (± 180 m) and riparian (Great Usutu river), while in the west it was also short (± 80 m) and riparian (also against the Great Usutu river). The sixth transect was 500-m long in natural savanna adjacent to the orchards. Sampling was at 100-m intervals, giving 129 sampling units overall. These were pooled into 12 sampling sites representing the orchards and various distances and habitat types from the orchards.

Sampling was monthly for 24 months using a beating tray supplemented by visual sampling. All species and life stages were collected and identified.

At each of the sampling sites, air temperature, relative humidity and percentage ground insolation were measured. Percentage ground insolation was used as a measure of the amount of sunlight penetrating through the vegetation and to which the insects were exposed. This was measured as a percentage of a 1 m^2 quadrat exposed to

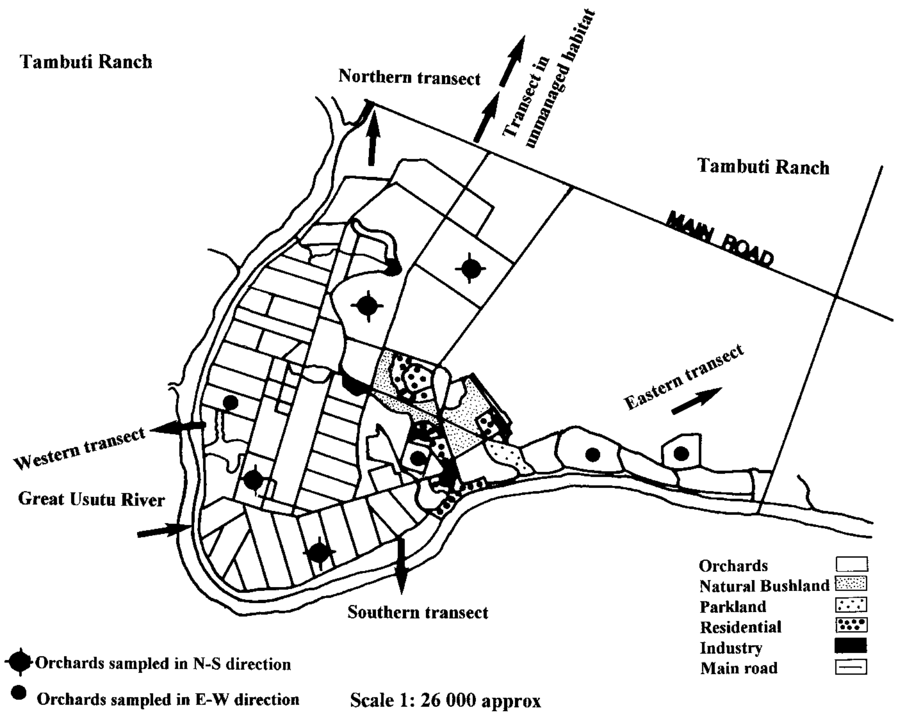

Figure 1. Map of the study site, showing position of the transects.

sunlight under the vegetation. The presence/absence of prey as well as the vegetation type on which the coccinellids were found was also recorded.

The coccinellid counts were $\log(x + 1)$ transformed, while the percentage data, i.e. relative humidity and ground insolation were arcsin transformed. Temperature data were untransformed. Statistical analyses were carried out using PRIMER and SPSS software packages. To minimize the effect of vagrant or rare species, those which contributed 3% or less to the total coccinellid densities were excluded from the final analyses (Clarke and Warwick 1994). Analyses of species distributions were carried out relative to location (north, east, west, south) and distance of sampling interval from the orchard habitat (100, 200, 300, 400 m).

Results

Whole assemblage

In total, 1645 coccinellid individuals in 31 species (including some unidentified adults) were collected from all sampling sites (Table 1). Monthly counts from all habitats sampled during the whole sampling period were used to calculate the cumulative

Table 1. Total coccinellid densities and species collected at Tambuti Estate during 1996/1998. 1 = orchards, 2 = eastern transect, 3 = northern transect, 4 = southern transect, 5 = western transect, 6 = habitat in bushveld. Numbers in bold represent species percentage in each habitat.

	Transect number					
Species	1	2	3	4	5	6
Coccinellinae						
Cheilomenes lunata (Fabricius)	183	67	30	21	10	47
	16.15	**51.54**	**36.14**	**21.88**	**16.95**	**32.14**
Cheilomenes propinqua (Mulsant)	16	1	0	0	0	0
	1.41	**0.77**	**0**	**0**	**0**	**0**
Declivata hamata (Schoenherr)	4	0	0	0	2	0
	0.35	**0**	**0**	**0**	**3.39**	**0**
Dysis decempunctata (Sicard)	0	1	0	0	0	0
	0	**0.77**	**0**	**0**	**0**	**0**
Hippodamia variegata (Goeze)	242	0	0	4	0	0
	21.36	**0**	**0**	**4.17**	**0**	**0**
Psyllebora variegata (Fabricius)	5	0	0	0	0	3
	0.44	**0**	**0**	**0**	**0**	**2.07**
Dysis sp.	72	6	0	0	0	13
	6.35	**4.62**	**0**	**0**	**0**	**8.97**
Coccidulinae						
Rodolia cardinalis (Mulsant)	127	0	0	0	0	0
	11.20	**0**	**0**	**0**	**0**	**0**
Rodolia sp.	6	0	0	0	0	0
	0.53	**0**	**0**	**0**	**0**	**0**
Novius sp.	4	0	1	0	0	0
	0.35	**0**	**1.20**	**0**	**0**	**0**
Chilocorinae						
Platynaspis capicola Crotch	11	2	0	2	0	0
	0.97	**1.54**	**0**	**2.08**	**0**	**0**
Chilocorus distigma (Fabricius)	4	0	0	0	0	0
	0.35	**0**	**0**	**0**	**0**	**0**
Brumus sp.	1	0	0	0	0	0
	0.09	**0**	**0**	**0**	**0**	**0**
Epilachninae						
Epilachna bifasciata (Fabricius)	11	0	0	0	1	0
	0.97	**0**	**0**	**0**	**1.69**	**0**
Epilachna paykulli Mulsant	2	0	0	3	10	0
	0.18	**0**	**0**	**3.13**	**16.95**	**0**
Epilachna hirta (Thunberg)	1	0	0	0	1	0
	0.09	**0**	**0**	**0**	**1.69**	**0**
Scymninae						
Ortalia ochracea Weise	6	0	0	17	0	5
	0.53	**0**	**0**	**17.71**	**0**	**3.45**
Scymnus prob. *levaillanti* (Mulsant)	89	2	0	19	12	0
	7.86	**1.54**	**0**	**19.79**	**20.34**	**0**
Scymnus sp.	283	42	44	21	8	54
	24.98	**32.31**	**53.01**	**21.88**	**13.56**	**37.24**
Nephus sp.	32	5	4	2	2	8
	2.82	**3.85**	**4.82**	**2.08**	**3.39**	**5.52**

Table 1. Continued.

	Transect number					
Species	1	2	3	4	5	6
Sticholotinae						
Pharoscymnus exiguus Weise	4	1	2	0	0	4
	0.35	**0.77**	**2.41**	**0**	**0**	**2.75**
Pharoscymnus uncosiphonalis Fursch	2	0	0	0	0	1
	0.18	**0**	**0**	**0**	**0**	**0.69**
Serangium sp.	7	0	1	0	0	0
	0.62	**0**	**1.20**	**0**	**0**	**0**
Unidentified larvae	7	0	0	0	2	2
	0.62	**0**	**0**	**0**	**3.30**	**1.38**
Unidentified pupae	4	0	1	2	3	5
	0.35	**0**	**1.20**	**2.08**	**5.08**	**3.45**
Unidentified adults	9	2	0	5	0	3
	0.80	**1.54**	**0**	**5.20**	**0**	**2.06**
Total number of individuals	1133	130	83	96	59	145
Total number of species	31	11	7	12	12	1

species counts for the overall coccinellid assemblage. There was a steady increase in the number of coccinellid species collected over the first year. After February 1997, there were fewer species additions, with an asymptote being reached in October 1997, eight months after the start of sampling.

Seasonal changes

Abundance was highest in February and lowest in November/December. There was a spring (August) increase in population densities the first year, which was not evident the following year. Despite the monthly variations in the numbers of individuals, species richness was relatively stable throughout the year.

There were no significant differences in the coccinellid population densities between the 2 years (ANOVA, $P = 0.191$). Data were thus combined in all subsequent analyses. The species rank-abundance curve indicated that the citrus was characterized by two dominant species, a few with intermediate densities, and many with only a few individuals.

Managed and adjacent natural habitats

The orchard habitat had significantly higher population densities than the natural habitats (ANOVA, $P = 0.004$). The orchards also had the highest number of species ($S = 31$). The natural habitats along the transects in the south and west had higher species diversity compared to those in the east and north (Figure 2a). The south and west sites were closer to the orchards and were bordered by the river.

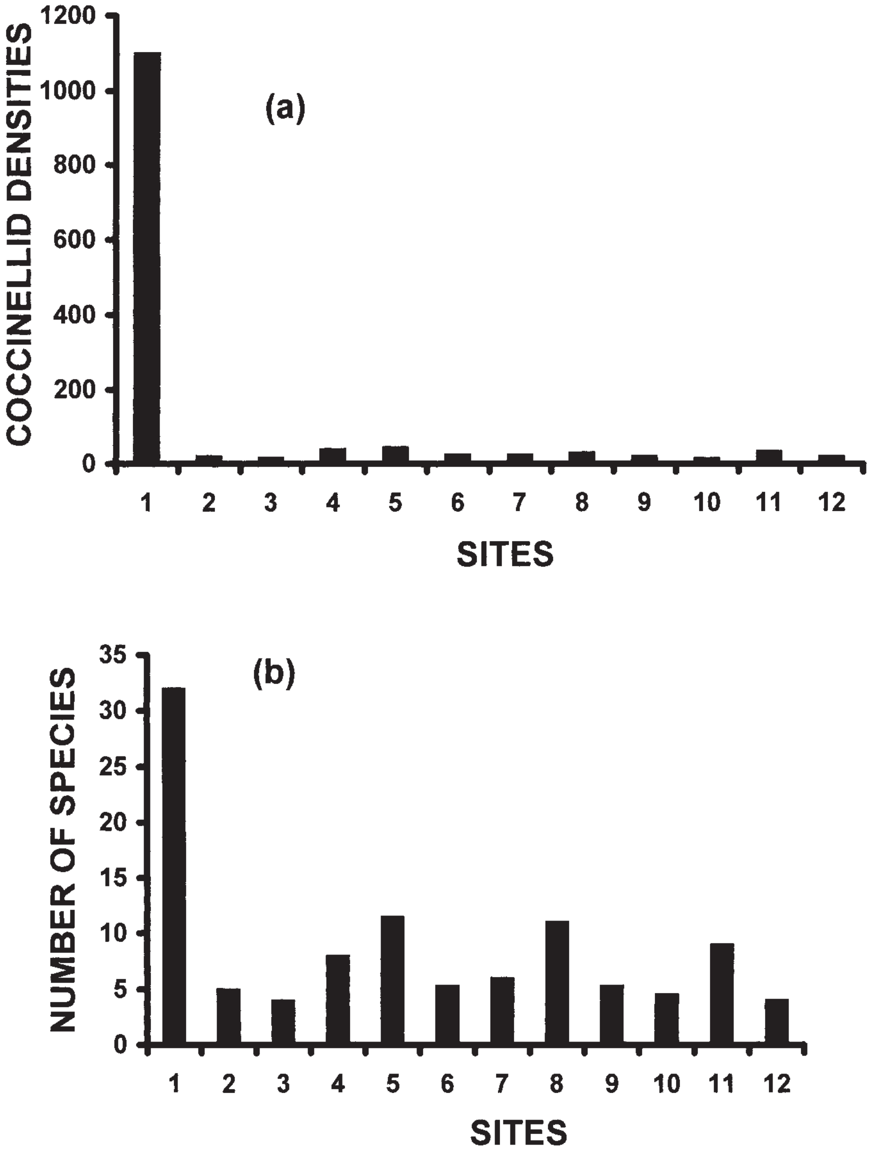

Figure 2. Coccinellid densities (a) and species richness (b) at each site. 1 = orchard, 2 = 100 m east, 3 = 100 m north, 4 = 100 m south, 5 = 100 m west, 6 = 200 m east, 7 = 200 m north, 8 = 200 m south, 9 = 300 m east, 10 = 300 m north, 11 = 400 m east, 12 = 400 m north.

The greatest species evenness was in the orchards, and natural habitats to the south and west of the orchards. Habitats on the northern and eastern sides of the estate had a few species represented by many individuals, a few with low numbers, but none with intermediate densities as in the orchards (Figure 2b).

Sites 300 and 400 m from the orchards had at least one dominant species and low numbers of other species. At 200 m, dominance by single species was still evident. At 100 m, species evenness was greater, with most species represented by intermediate values compared to sites farther away. The orchards had greatest species evenness.

The total average densities from each sampling interval, rather than individual sampling sites, were used to make the data more interpretable (Clarke and Warwick 1994). The resultant dendogram indicated that the sites could be divided into three distinct groups at the 50% level of similarity (Figure 3). The first group consisted of the orchards and sites at 100 m from the orchards at the southern and western boundaries. Species common to sites in this group were *Scymnus* prob. *levaillanti*, *Cheilomenes lunata*, *Epilachna paykulli*, *Scymnus* and *Nephus* sp. The group divided further so that the sites within the orchards were separated from the two sites at the river borders. The orchards were characterized by *Rodolia cardinalis*, *Chilocorus*

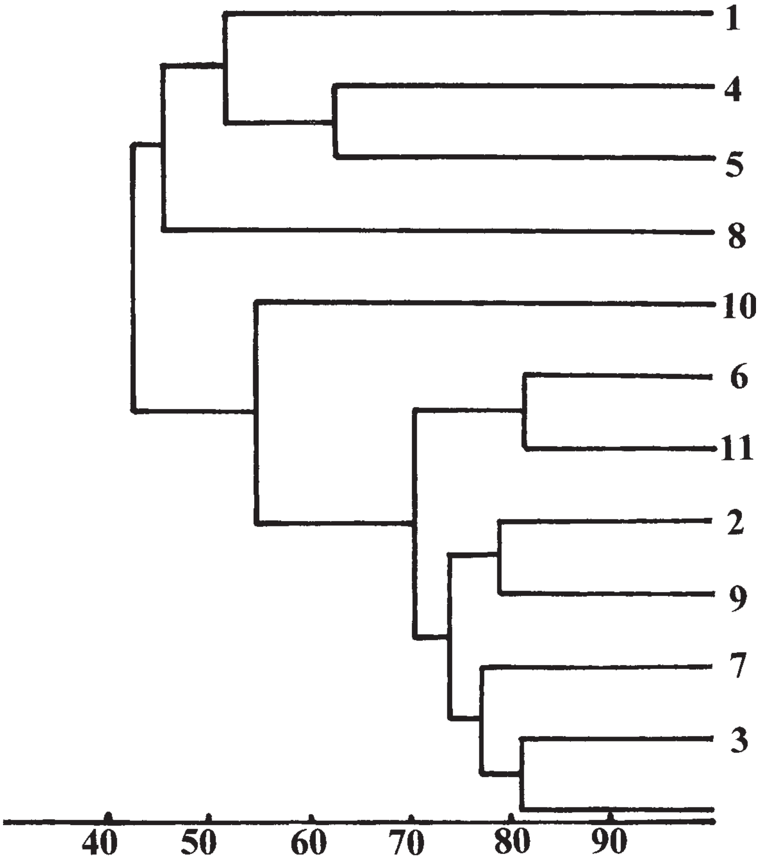

Figure 3. Cluster analysis of sites based on their coccinellid assemblages. 1 = orchard, 2 = 100 m east, 3 = 100 m north, 4 = 100 m south, 5 = 100 m west, 6 = 200 m east, 7 = 200 m north, 8 = 200 m south, 9 = 300 m east, 10 = 300 m north, 11 = 400 m east, 12 = 400 m north.

distigma, *Brumus* sp., and *Hippodamia variegata*. The southern sites at 200 m formed the second group, with species common in this group being *Platynaspis capicola*, *Ortalea ochracea*, *C. lunata*, *E. paykulli*, *Scymnus* and *Nephus* sp. The third group comprised all sites at the intervals in the northern and eastern habitats. Species common to sites in this group were *Pharoscymnus exiguus, C. lunata, Scymnus* sp. and *Nephus* sp. This further divided with the site at 300 m north separating off. The rest of the sites in the northern and eastern transects formed a cluster. Differences between sites were also indicated by ANOVA ($P = 0.02$), where the orchard coccinellid densities were significantly different from those in the natural savanna habitats, i.e. northern and eastern boundaries ($P = 0.05$). NMDS ordination also placed the sites into groupings similar to those of the dendogram (Figure 4).

Temperature was highest in the natural habitats (north and east) and in the orchards, while lowest in the sites near the river (west and south). Temperature was negatively correlated with coccinellid densities ($r = -0.312$, $P = 0.05$). Relative humidity was highest at sites near the river. Lowest relative humidity was in the northern and eastern habitats, which were farthest from the irrigated orchards and river. Correlation between coccinellid densities and %RH was 0.303 ($P = 0.054$). Ground insolation was lowest at sites with more vegetation cover, i.e. the orchards and river borders (western) habitats. The natural savanna sites had the highest insolation, especially in winter when there was minimal vegetation growth. Although not statistically significant, coccinellid densities were negatively correlated with insolation ($r = -0.217$, $P = 0.174$).

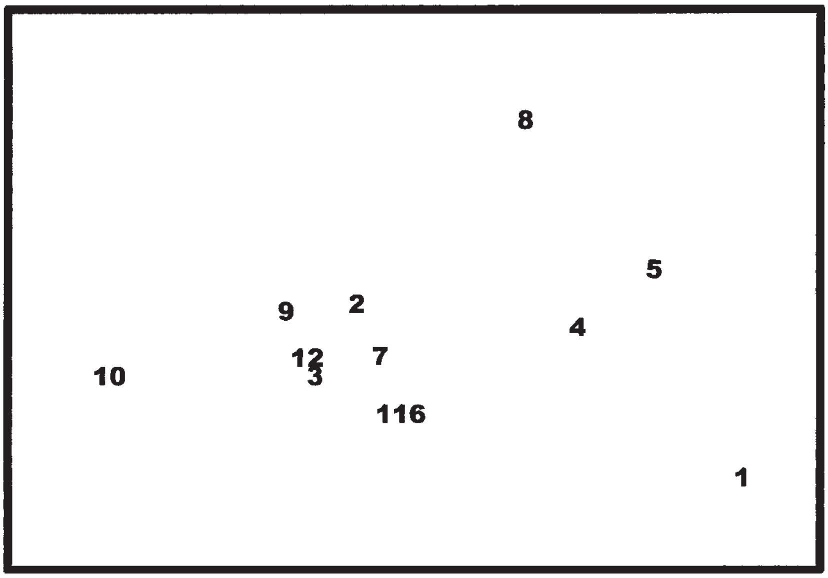

Figure 4. Non-metric multidimensional sealing ordination plot of the 12 sites. 1 = orchard, 2–12 = sites outside the orchard.

The majority of sites had coccinellids associated with prey at some time during the year. However, no prey was observed at the sites on the west or on trees which were more than 300 m from the estate in all directions. Prey was significantly correlated with coccinellid densities $r = 0.379$, $P = 0.014$).

Simple multiple regression was also used to further test the significance of the environmental and prey variables. The model was significant ($P = 0.025$), where the temperature, insolation and relative humidity had no significant impact on coccinellid densities, while the presence/absence of prey was significant ($t = 2.740$, $P = 0.0095$).

Natural savanna matrix

The natural savanna had low species evenness and was characterized by two, very abundant species and several rare ones, which was also confirmed when the species abundance per sampling interval was analyzed. All the sites at the various sampling intervals were characterized by one abundant species. The first four distance–intervals had moderately abundant species and also some rare ones.

Species distribution did not vary significantly between the sampling intervals ($P = 0.920$), with species richness and population densities being relatively uniform throughout the overall sampling area (Figures 5 and 6). None of the variables, i.e. prey ($r = 0.228$, $P = 0.415$), %RH ($r = 0.197$, $P = 0.481$), temperature ($r = -0.197$,

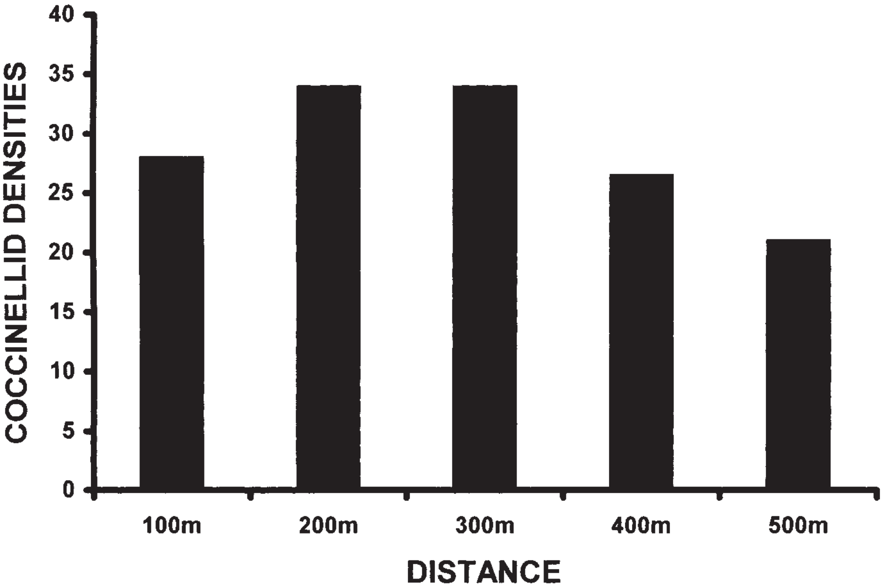

Figure 5. Coccinellid population density per site at each sampling interval in the indigenous vegetation habitats.

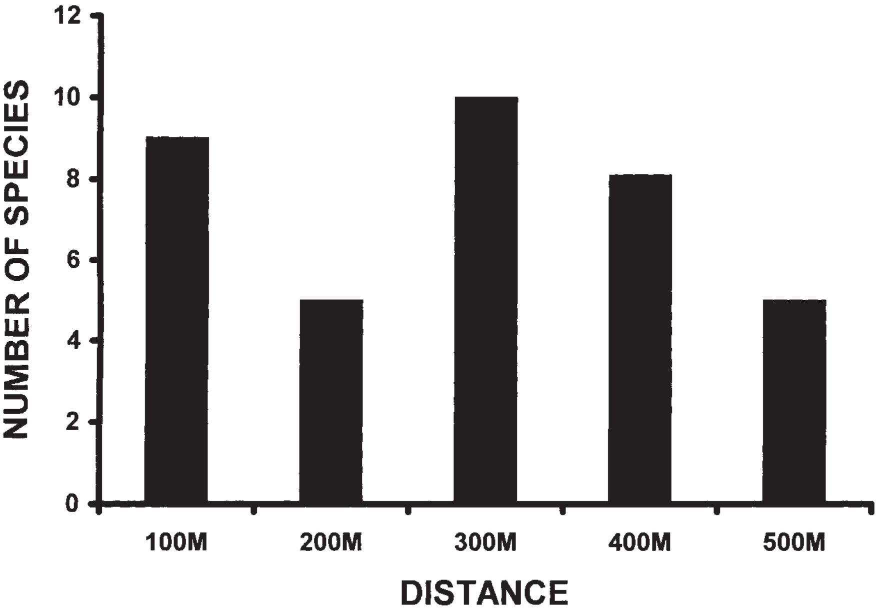

Figure 6. Coccinellid species richness per site at each sampling interval in the indigenous vegetation habitats.

$P = 0.481$) and insolation ($r = -0.076$, $P = 0.787$), was significantly correlated with densities.

Discussion

Coccinellid distribution across the land mosaic

The orchard had higher coccinellid densities and species richness than did the natural habitats. The orchards also had the greatest species evenness, with no markedly dominant species. Duelli (1988) also observed that the highest diversity and density of coccinellid species were within managed crop systems, followed by the semi-natural habitats, e.g. hedgerows and river borders, and the lowest in the natural habitats. This study, the first of its kind in Africa, corroborated the distribution patterns observed in Europe. The vegetation-rich, riparian habitats also had high coccinellid and prey densities, but not quite as high as in the orchards. In contrast, the dry, savanna vegetation, was poor in species and numbers of individuals.

The abundance of prey species, e.g. aphids, *Icerya purchasi*, *Aonidiella aurantii*, (in the case of predaceous coccinellids) in the orchards was a major factor contributing to the distribution pattern of the coccinellids. Coccinellid presence is known to be determined by the presence of suitable prey (Hodek 1973; Majerus and Kearn

1989), so long as the prey is not so abundant that it is irreparably damaging the plant host (Erichsen et al. 1991). This has economic advantages, since coccinellids, e.g. *Rodolia* sp. and *C. distigma* usually have corresponding distributions (Hagen 1962). Coccinellids in managed habitats are however, more likely also to suffer from crop management effects, such pesticide applications, mowing, pruning and harvesting.

That certain species were present throughout all sampling sites suggests that there is movement between habitat patches. The ability of species like *C. lunata*, *Nephus* sp. and *Scymnus* sp. to move in this way enhances their role in pest management, as they seek spots of high prey density. Also, these mobility patterns enhance the value of natural habitats (especially riparian ones) in that orchards are re-invaded. Since these ladybirds reproduce in both natural and orchard habitats at this citrus estate, both habitat types have high residence value in the landscape mosaic. An important criterion in the determination of suitable coccinellid habitat is the species' ability to reproduce in that habitat. Adults are poor indicators of favourable habitats due to their high mobility and they may occur in a non-typical habitat in search of prey (Hodek 1967, 1973).

The dominant species or species assemblages in each habitat type were not good indicators of that habitat type. In the orchards, species like the exotic *Hippodamia variegata*, *C. lunata*, and indigenous *Scymnus* sp. dominated. *Hippodamia* and *Cheilomenes* species are aphid feeders and occur in high numbers where there are high numbers of prey (Johki et al. 1988; Majerus and Kearn 1989), as was the case here. Relatively higher population densities were found in the orchards where there was also greater plant diversity, e.g. herbs, grasses, citrus trees. Although not as abundant as in the orchards, *C. lunata* also occurred on grasses in the natural habitat and river borders, especially after rains. This pattern of widespread occurrence was, however, not consistent, since few of these coccinellids were observed in the natural habitats during the second year of sampling, illustrating the highly dynamic nature of these beetles' populations.

Scymnus sp. and *C. lunata* were dominant across all sites and may be considered to be multihabitat species (Forman 1995). Their distribution seemed to be determined largely by the presence of their prey species, scale insects and aphids, respectively.

Throughout the sampling period, the economically-important but exotic *Rodolia* sp. and indigenous *Chilocorus distigma* were only in the managed habitats. Restriction of economically important species to managed habitats has also been observed in Europe where a quarter of carabid beetles species were found only in arable fields, and the occurrence of 40 to 60 different species of carabids, staphylinids and spiders in the crop system is considered as normal (Booij and Noorlander 1992).

Some species were associated with specific habitats, e.g. indigenous *Epilachna paykulli* was found only in the managed and riparian habitats. This species was absent in the dry, hotter sites where its hosts were absent. In contrast, indigenous *Pharoscymnus exiguus* and *Dysis* sp. occurred only on trees both in the orchard and in the natural savanna, despite less prey.

Contributing factors to local coccinellid distribution

While coccinellid distribution was not indicative of a particular habitat, most were found on specific vegetation type. Species known to be phytophagous, e.g. *Epilachna* spp. were always on short curcubit or solanaceous plants. Species associated with scale insects, e.g. *Scymnus* sp. and *Nephus* sp., were found mainly on prey-infested shrubs in the savanna and on citrus. Association of a coccinellid species with a prey species however, does not necessarily indicate that it is feeding on that prey (Majerus 1994).

The aphidophagous species were not restricted to any particular vegetation type in most of the managed habitats and occurred on trees, herbs and grasses. Yet in the savanna, they were restricted to grasses. Of the dominant aphidophagous species, only *C. lunata* was widespread across the agricultural mosaic. In contrast, *H. variegata* was restricted to orchards, which is in contrast to the Ukraine where adults of the species were found across a range of habitats (Hodek 1967).

Not all the coccinellids in the present study were associated with prey, e.g. *Dysis* sp., *P. exiguus*, and *Ortalia ochracea*. Although species like *O. ochracea* were occasionally found on citrus trees, no prey was with them, as was also the case in the savanna.

There was not the distributional correlation between coccinellid and prey in the savanna as in the orchards. In the savanna, food supply is unreliable with little or no prey, and for the phytophagous species there is less extensive vegetational growth to attract them. In these natural habitats, the coccinellids appear to be highly vagile, seeking out small pockets of prey or suitable vegetation, especially in the orchards.

Abiotic environmental variables

The abiotic environmental variables measured did not have any statistically significant effects on coccinellid densities. The high relative humidity sites adjacent to the river and in the irrigated orchards had variable influence on different coccinellid species. *Coleomegilla maculata*, for example, increased in the orchard, while *Hippodamia convergens* was apparently insensitive to the same variable (Hodek 1973). Temperature and ground insolation had no significant effect on the species or their abundances. However, *C. lunata*, *H. variegata* and *Dysis* sp. were mostly in well-insolated areas such as grass and herbs in direct sunlight. Species on the citrus or indigenous trees were in a cooler environment with very little insolation. Furthermore, the multiple regression analysis clearly indicated the weak influence of abiotic variables, in contrast to the importance of prey. Although not significant, temperature and insolation was negatively correlated with coccinellid densities. This was in agreement with field observations that fewer coccinellids were observed during the hottest hours or in highly-insolated areas.

Significance of habitat heterogeneity

Results suggest that the orchards are favourable habitats within the less favourable natural savanna for coccinellids. Not surprisingly, this is especially so for the economically-important species. The presence of coccinellid species in both the natural and managed habitats emphasizes the importance of maintaining a heterogenous array of habitats which are utilized by generalist species such as *Cheilomenes* spp., *Scymnus* sp., *Nephus* sp. and which promote their beneficial use in the agricultural landscape. While easily sampled, coccinellids apparently do not constitute good indicators of habitat, probably due to their distribution generally being dependent on prey availability rather than on habitat characteristics. Nevertheless, a variety of vegetation types appears to be essential for generating coccinellid diversity and for prey regulation. Plant diversity and coccinellid mobility are often interlinked, and furthermore, the beetles need complementary food sources, e.g. pollen and nectar from various wild flowers spread throughout the natural habitats (Burel and Baudry 1995). Indeed, it seems that some species thrive on an array or mosaic of habitats. In general, the heterogenous land mosaic encourages the enrichment of the coccinellid assemblage, which contributes to biodiversity enhancement and pest regulation. The results here, besides illustrating that agricultural patches are not necessarily comparatively poor in species, also emphasize the need to ensure linkages between the patches for passage of beetles between the various mosaic elements.

The value of this agricultural land mosaic for coccinellid diversity does not of course mean that all ‘quality’ biodiversity is being maintained. Indeed, some of the ladybirds were exotic. Furthermore, the Coccinellidae is possibly one of the most tolerant of taxa to transformed landscapes. Nevertheless, there is a clear pointer here that it would be hasty to dismiss certain agricultural transformation of the savanna as the antithesis of biodiversity conservation. There is now a need to investigate what other components of biodiversity are being maintained or lost through such landscape change.

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