

Species interslope divergence of ants caused by sharp microclimatic stresses at 'Evolution Canyon' II, Lower Nahal Keziv, western Upper Galilee, Israel

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ABSTRACT

Species diversity of ants was recorded in 2000–2001 at seven stations of a microsite in Nahal Keziv, western Upper Galilee, designated as 'Evolution Canyon' II. In the 7000 m² area, we recorded 31 ant species including one species identified only at the genus level: 19 on the 'African' slope, 12 on the 'European' slope, and 17 species at the valley bottom. Among the recorded species one is new to the fauna of Israel (*Cataglyphis semitonsus*). Interslope ant species composition varies remarkably due to differential microclimatic conditions, partly demonstrating the effect of microclimate differences on ant species diversity at a microscale. Further studies at this site following the 'Evolution Canyon' model as conducted at EC I in Mount Carmel, will enable in-depth investigations of changes in biodiversity, adaptation and incipient sympatric speciation, i.e. *evolution in action*, within a relatively free breeding interslope populations.

KEYWORDS: Formicidae, ants, species diversity, Israel, 'Evolution Canyon' model, microclimate.

INTRODUCTION

Biodiversity patterns and evolution

Measuring and maintaining biodiversity of all life forms is of high importance (Wilson 1992) and demands understanding of all organisms, their biology, evolution, ecology and the biogeography of particular groups and species. Of equal importance is understanding of underlying evolutionary and ecological processes and patterns. Israel is situated in the south of the Levant, which is one of the most complicated ecosystems in the world that includes plant and animal taxa from the Palearctic Afrotropical, and Oriental regions. The Levant might be considered as one of the richest and most diverse natural areas in the temperate regions of the world relative to its size (Tchernov and Yom-Tov 1988). This study deals with local differences in ant species diversity and composition between the opposing slopes of 'Evolution Canyon' II, lower Nahal Keziv [נהל כזיב], western Upper Galilee, Israel (33°02'N 35°11'E), and the local and regional patterns resulting from differential microclimate selection pressures. The ecological theater of this study is the 'Evolution Canyon' model (Nevo 1995, 1997, 2006, 2012).

The 'Evolution Canyon' model: a microcosm of life's evolution

Biodiversity evolution studies requires more critical tests at local microgeographic sites subdivided by sharp ecological contrasts. These microscale natural evolutionary laboratories reveal dramatic interslope divergence in genes, genomes, populations,

species, ecosystems, and biota (Nevo 2001). In the long-term research projects at the 'Evolution Canyon' I (EC I) microsite, lower Nahal Oren, Mount Carmel (32°43'N 34°58'E), studied since 1991, and 'Evolution Canyon' II (EC II) microsite, studied since 1998, we made generalizations across life and organizational levels in an attempt to highlight controversial and unresolved problems of biological evolution (Nevo 1995, 1997, 2001, 2006, 2009, 2011, 2012; Finkel *et al.* 2002). The south-facing, or 'African', slopes (SFS) of 'Evolution Canyons' I, II, III, and IV in the mountains of Carmel, Galilee, Negev and Golan, respectively, receive higher solar radiation (as other canyons north of the equator across the planet) than nearby north-facing, or 'European', slopes (NFS) (Shreve 1922; Cottle 1932; Stephenson 1982). This solar radiation associated with higher temperature and drought on the 'African' slope (Pavliček *et al.* 2003) causes remarkable physical and biotic contrasts at a microscale. If rocks, soil, and topography are similar on the opposite slopes, the *microclimate* remains the major interslope divergence factor of biodiversity. The 'African' slope is richer than the 'European' slope in such taxa as bacteria, plants, and animals. In comparison, the 'European' slope is richer than the 'African' slope in reproductively humidity-dependent lower plants and fungi, thus locally displaying regional and global patterns despite the possibility of mixing by easy migration across the microsite. To date, we have identified more than 2500 species in EC I, many of which display qualitative or quantitative divergences between and within slopes (Nevo 1995–2012). In EC II, we recorded more than 1000 species of organisms up to 2003 (Vinogradova *et al.* 2000; Finkel *et al.* 2001, 2002; Grishkan *et al.* 2003).

'Evolution Canyon' II, lower Nahal Keziv

'Evolution Canyon' II is presumably several million years old, i.e. is of a Plio-Pleistocene origin. It is eroded in the uplifted Upper Cenomanian limestone block in the Mediterranean climate (Matmon *et al.* 2000, 2003). The EC II soil is alkaline with maximal pH in the 'African' slope ($\text{pH}=8.09 \pm 0.20$), and minimal pH in the Valley Bottom (VB) ($\text{pH}=7.36 \pm 0.14$). Organic matter content and moisture content were highest in the VB soil and lowest in the 'African' slope soil (Grishkan *et al.* 2003). The opposite slopes of EC II, separated by only 50 m at bottom and 350 m at top, display remarkable biotic contrasts and divergence due to up to 700% (in EC I it is 800%!) higher solar radiation on the 'African' slope than on the 'European' slope. The average annual rainfall is 700 mm (Matmon *et al.* 2000), with no known interslope differences in rainfall, though such interslope differences have been recorded elsewhere (Sharon 1970, 1980; Sharon *et al.* 1983; Sharon and Arazi 1997). Rainfall measurements conducted at the Elon Meteorological Station, situated 4 km northeast of EC II (300 m a.s.l.), during the research years showed the following results: September 1999–September 2000, 688 mm; September 2000–September 2001, 538 mm (Israel Meteorological Information Center 2014).

Spatiotemporally, the 'African' slope represents a 'broader-niche' (*sensu* Van Valen 1965), with garrigue (shrub community) and dry, 'savanna-like' biotas. Spa-

tially the ‘African’ slope consists of more microhabitat patches and subdivisions than the ‘European’ slope. Notably, small variations in aridity in the *Calicotome villosa* Poiret (Papilionaceae [Fabaceae]) and *Salvia fruticosa* Miller (Labiatae [Lamiaceae]) garrigue at the lower part and the dry, Mediterranean–African, ‘savannoid’, open park forest of *Ceratonia siliqua* L. (Caesalpiniaceae) and *Pistacia lentiscus* L. (Anacardiaceae) at the top of the slope amplify the biotic divergence of the other taxa on the ‘African’ slope, both in space and over time. By contrast, the milder, cooler, and more homogeneous ‘European’ slope is covered by a dense forest of *Acer obtusifolium* J.E. Smith, or Syrian Maple (Aceraceae) and *Laurus nobilis* L. (Lauraceae) with no grassland openings (Finkel *et al.* 2001).

MATERIALS AND METHODS

Topography and sampling stations

The ‘African’ slope dips at 20–40° and includes sampling stations 1, 2, and 3 at altitudes of 200, 170, and 140 m above sea level, respectively. Station 4 is at the valley bottom at 110 m a.s.l. There is only one station at the narrow VB and, therefore, it is under-sampled compared to the slopes. The ‘European’ slope dips at 30–40° and includes sampling stations 5, 6 and 7 at 140, 170 and 200 m a.s.l., respectively. All these stations are parallel to the seasonal summer-dry riverbed on the VB (Fig. 1).



Fig. 1: ‘Evolution Canyon’ II microsite in Nahal Keziv, western Upper Galilee, Israel. A cross section. Higher solar radiation on the ‘African’ south-facing slope (SFS) causes warm, xeric, garrigue, Mediterranean–African, “savannoid” plant formation habitats versus cool, mesic, dense, “south-European” maquis forest on the ‘European’, north-facing slope (NFS).

Collection methods

The ants were collected by two methods: (1) with pitfall traps (inner diameter 8 cm, depth 10 cm) filled with ethylene glycol (Chikatunov *et al.* 1997); ten traps were placed in a line along each station at the 10 m distance between neighboring traps; the traps operated over a 12-month period, from October 2000 to October 2001, and were emptied every 2–4 weeks; (2) manually in the summer of 2000 and winter, spring, and summer of 2001; each manual collection sampled the SFS, VB and NFS with same collection duration. Ants were preserved in 70% ethanol.

Statistical analysis

Chi-square tests for independence of attributes were conducted using the JMP version 10.0 statistical package (SAS Institute 2012). We run into the problem of small expected values. Cochran (1952, 1954) concluded that if all the expectations are not less than two, the approximation is acceptable. By 'acceptable' he meant that the exact probability is between ± 0.01 around $p=0.05$ and between 0.007 and 0.015 for $p=0.01$. Roscoe and Byars (1971) concluded that there is no experimental justification for the common rule of thumb that 'expectation more than five' are needed (they cited also Tate and Hyer (1969), supporting this statement). These authors suggested that expected values of two or more are sufficient. Lewontin and Felsenstein (1965) studied the χ^2 test for homogeneity with five degrees of freedom and more. The only case when they got a serious non-conservative deviation was when the expectations included a value of 0.05. They concluded that it is robust and safe to use the χ^2 test when expectations do not include fractions. We follow here their recommendations.

RESULTS AND DISCUSSION

Interslope species biodiversity

Thirty one ant species were recorded from EC II (Table 1), almost 15% of the 203 ant species of Israel (Vonshak and Ionescu-Hirsch 2009). One of them, *Cataglyphis semitonsus*, is new to the Israel fauna. Three species are first reported from Upper Galilee, viz. *Crematogaster auberti nigripes*, *Lepisiota opaciventris* and *Tetramorium taueret*. Nineteen species were recorded from the 'African' slope versus 12 from the 'European' slope. Seventeen species were found on the valley bottom (Fig. 2). There are only eight species common to both slopes (34.8% of the ant species found on both slopes, Jaccard similarity index 0.348). Considering only the *slope-unique* species (nine on the SFS and three on the NFS) the interslope unique species differences is not significant (binomial test $p=0.073$). When considering the species which appear on one slope (either SFS or NFS) and at the VB [11 at SFS+VB vs 4 at NFS+VB] the binomial test is: ($\chi^2_{(1)}=4.26$, $p<0.05$), based on the species richness of the opposite slopes.

Local and world distribution and zoogeographical elements

Most of the species (20/31) are distributed in the south, center and north of Israel. Four species are distributed only in northern Israel. Twenty-six species

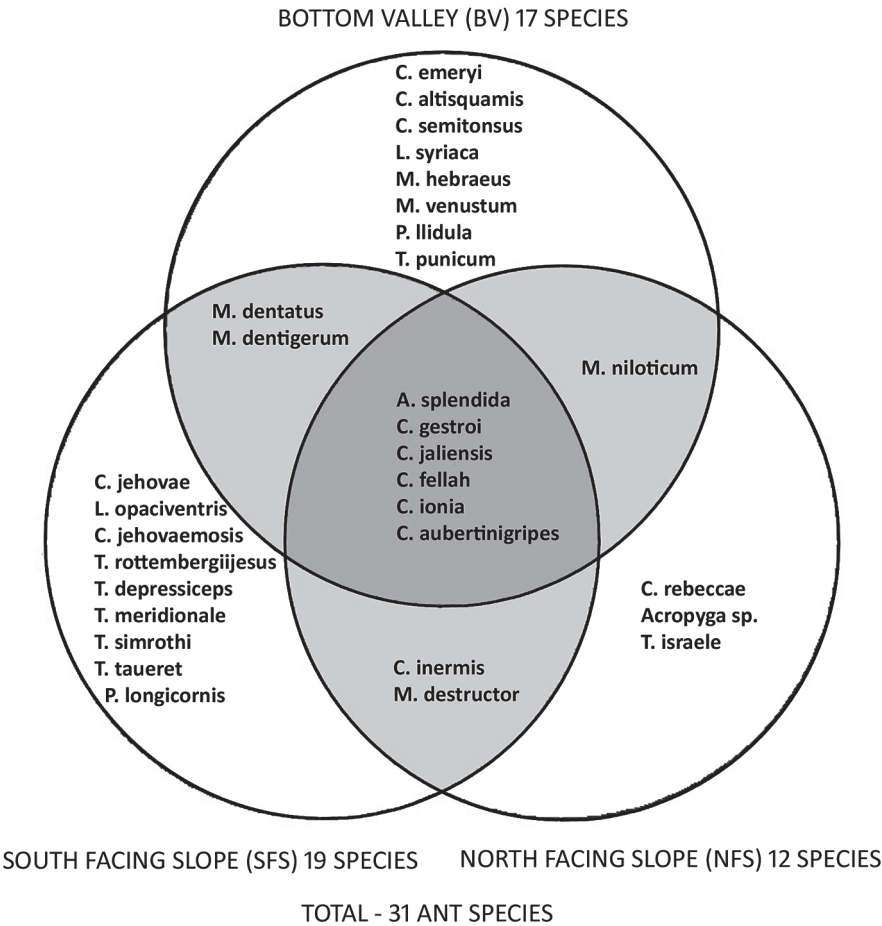


Fig. 2: Venn diagram of ant species at ‘Evolution Canyon’ II.

were found also in Lebanon (three of them are cosmopolitan or found in all Mediterranean countries, according to Tohmé (1969)). Eight species were found also in Saudi Arabia (Collingwood and Agosti 1996). No statistical correlation was found between the slopes and regional distribution or zoogeographical elements of the world. However, it is worth noting that two species, *Lepisiota opaciventris* and *Tetramorium depressiceps* that range to Saudi Arabia (Vonshak and Ionescu-Hirsch 2009) were collected only on SFS. Also, the fragmentary ecological data available on the species found in this research partly connects the slope’s species distribution to their known habitat preference:

- *Crematogaster jehovae mosis* which has been found only on the SFS is associated with the arid environments genus *Tamarix* Galls (Ofer 2000). However,

Table 1: The List of ant species collected in the ‘Evolution Canyon’ II (EC II) and their distribution in the EC II, in Israel, and in other Mediterranean countries. Abbreviations: EC II: NFS – north-facing slope, SFS – south-facing slope, VB – valley bottom. In Israel (after Ofer (2000) and Vonshak and Ionescu-Hirsch (2009)): N – North (north of Mt. Carmel and Mt. Gilboa), C – Center, S – South (south of northern Negev and Dead Sea Valley). Zoogeographical elements (after Kugler (1988)): CM – Circum-Mediterranean, EM – East Mediterranean, NEM – North-East Mediterranean, C – cosmopolitan, Pantropical, En – endemic to Levant, Er – eremic or Saharo-Arabian, IT – Irano-Turanian. Distribution in other Mediterranean countries is given after Tohmé (1969), Kugler (1988) and *AntWiki*.

No.	Species	Distribution					Zoogeographical element
		EC II			Israel	Other Mediterranean countries	
		SFS	VB	NFS			
1	<i>Aphaenogaster splendida</i> Roger	+	+	+	C, N	All	CM
2	<i>Camponotus gestroi</i> Emery	+	+	+	N	All	CM
3	<i>C. jaliensis</i> Dalla Torre	+	+	+	S, C, N	All	CM
4	<i>C. fellah</i> Dalla Torre	+	+	+	S, C, N	Syria, Turkey, Lebanon, Egypt	EM
5	<i>C. rebecca</i> Forel			+	S, C, N	Lebanon, Syria	EM
6	<i>Cardiocondyla emeryi</i> Forel		+		S, C, N	Egypt	C
7	<i>Cataglyphis altisquamis</i> (André)		+		N	Lebanon, Syria	EM
8	<i>C. semitonsus</i> Santschi		+		N	Lebanon, Algeria	?
9	<i>Crematogaster ionia</i> Forel	+	+	+	C, N	Greece, Turkey, Lebanon	NEM
10	<i>C. auberti nigripes</i> Menozzi	+	+	+	S, C, N	Libya	Er
11	<i>C. inermis</i> Mayr	+		+	S, C, N	Spain, Lebanon, Egypt	Er
12	<i>C. jehovae jehovae</i> Forel	+			S, C, N	Greece, Lebanon, Egypt	EM
13	<i>C. jehovae mosis</i> Forel	+			S, C, N	Lebanon	En
14	<i>Lepisiota syriaca</i> André		+		C, N	Lebanon, Syria, Egypt, Turkey	EM
15	<i>L. opaciventris</i> Finzi	+			S, N	Egypt	Er

Table 1 (continued): The List of ant species collected in the 'Evolution Canyon' II (EC II) and their distribution in the EC II, in Israel, and in other Mediterranean countries.

16	<i>Temnothorax rottembergii</i> jesus Forel	+			S, C, N	Lebanon, Turkey	EM
17	<i>Messor dentatus</i> Santschi	+	+		S, C, N	Lebanon	En
18	<i>M. hebraeus</i> Santschi		+		S, C, N	Lebanon	EM
19	<i>Monomorium dentigerum</i> Roger	+	+		S, C, N	Lebanon, Syria	EM
20	<i>M. destructor</i> Jerdon	+		+	S, C, N	Spain, Lebanon	C
21	<i>M. niloticum</i> Emery		+	+	S, C, N	Lebanon, Egypt	Er
22	<i>M. venustum</i> Smith		+		S, C, N	Lebanon, Syria	EM
23	<i>Paratrechina longicornis</i> Latreille	+			S, C, N	Cosmopolitan	C
24	<i>Pheidole pallidula</i> Nylander		+		S, C, N	All	CM+IT
25	<i>Acropyga</i> sp.			+	N		
26	<i>Tapinoma israele</i> Forel			+	C, N	Lebanon	
27	<i>T. simrothi phoeniceum</i> Emery	+			S, C, N	Cyprus, Lebanon	CM
28	<i>Tetramorium taueret</i> Bolton	+			S, C, N	Egypt	
29	<i>T. depressiceps</i> Menozzi	+			S, N	Lebanon, Egypt	EM
30	<i>T. meridionale</i> Emery	+			C, N	All except for South	CM
31	<i>T. punicum</i> (Smith)		+		S, C, N	Egypt, Greece, Turkey, Syria, Lebanon	EM
TOTAL:		19	17	12			

C. jehovae mosis and *C. jehovae jehovae* are considered arboreal species by Tohmé (1969).

- *Paratrechina longicornis* found only on the SFS builds nests in open terrain under stones (Ofer 2000) and may avoid forest environments.
- *Tapinoma simrothi phoeniceum* has been found nesting in open spaces with high insolation, only on the SFS. This species is associated with aphids found mainly on cereals and shrubs which characterize relatively open spaces as the SFS (Ofer 2000). On the contrary, *T. israele* which was found only on the NFS, is a hydrophilic species and prefers shaded habitats and lower temperatures.

- *Monomorium niloticum*, found on the NFS and VB, is known in Saudi Arabia mainly in agricultural and irrigated areas and not on desert sands (Collingwood and Agosti 1996).
- *M. dentigerum*, found on the SFS and VB, has been recorded by in northern Israel in open, low shrub and grassland habitats and not in open maquis or road sides, while *M. destructor*, found on both slopes, was found in all those three habitats (Martinez 2008).
- Three of the four *Tetramorium* species have been found only on the SFS and one, on the VB. Little ecological data are available for these species, but according to Tohmé (1969), *T. meridionale* nests only in dry exposed places. It is worth noting that in research conducted in Spain, the three *Tetramorium* species that were found on SFS “were strongly associated with sites with high temperatures” (Arnan *et al.* 2012).

CONCLUSIONS

We may conclude that: (1) Species diversity of ants is higher on the ‘tropical’, ‘African’ slope, paralleling the latitudinal gradient of biodiversity distribution (Schall and Pianka 1978), i.e. increasing species richness in tropical areas. This phenomenon is due probably to greater spatial and temporal heterogeneity and, consequently, larger numbers of ecological niches on the SFS. The same phenomenon has been found for ants on the opposite slopes of a valley in the Judean Hills (Ofer *et al.* 1978) and in ‘Evolution Canyon’ I in the Carmel Mountains (Ofer *et al.* 1996). It has also been observed in other terrestrial groups in EC II (Coleoptera, 307 species recorded from the ‘African’ vs 198 from the ‘European’ slope (Finkel *et al.* 2002); Cyanoprocarota: the ‘African’ slope harbored 29 species, the ‘European’ slope only 17 (Vinogradova *et al.* 2000); soil microfungi: 149 species have been isolated from the ‘African’ slope, only 78 from the ‘European’ slope (Grishkan *et al.* 2003); plants: 205 species were recorded from the ‘African’ slope vs only 54 from the ‘European’ slope (Finkel *et al.* 2001)).

(2) Interslope species composition was different, with marked slope unique species, in spite of the remarkably small distance between the slopes. The available evidence suggests that climatic selective constraints, overriding migration and stochasticity seem to be, in ants, as in other organisms in the canyon, the major adaptive evolutionary divergence force (Nevo 2011). Microclimate (and consequently vegetation), seems to be the major driving forces because rocks and soil are similar on both slopes.

The ‘Evolution Canyon’ model is ideal to analyze biodiversity evolution at a microscale due to interslope divergent microclimates. This remarkable pattern could be extended and tested with additional taxa across phylogenies of other taxa. Likewise, additional *proteomic*, *genomic*, and *phenomic* studies could be conducted with this ant fauna as well as on other groups in ‘Evolution Canyon’ II in order to identify such climatic effects on other biological aspects. In particular proteomic

and genomic perspectives could provide the basis for interslope adaptive complexes as was shown in the annual plant *Ricotia lunaria* L. (Cruciferae [Brassicaceae]) at EC I (Brodsky *et al.* 2008; Kossover *et al.* 2009) and in *Drosophila melanogaster* Meigen (Drosophilidae) at EC I (Hubner *et al.* 2013) (see also an overview on adaptive complexes at EC in Nevo (2012)). Finally, in-depth investigations should be performed on possible interslope incipient sympatric speciation in ants, as has been shown in EC I in soil bacteria (Sikorski and Nevo 2005), wild barley (Parnas 2006; Nevo 2006), *Drosophila melanogaster* (Korol *et al.* 2006), and spiny mice *Acomys cahirinus* Geoffrey (Muridae) (Hadid *et al.* 2013). The ‘Evolution Canyon’ microsites in Israel, and elsewhere in the world, could be ideal for studying *evolution in action*.

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