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Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions

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Summary

1. Valuable insights into mechanisms of community responses to environmental change can be gained by analysing in tandem the variation in functional and taxonomic composition along environmental gradients.

2. We assess the changes in species and functional trait composition (i.e. dominant traits and functional diversity) of diverse bee communities in contrasting fire-driven systems in two climatic regions: Mediterranean (scrub habitats in Israel) and temperate (chestnut forests in southern Switzerland).

3. In both climatic regions, there were shifts in species diversity and composition related to post-fire age. In the temperate region, functional composition responded markedly to fire; however, in the Mediterranean, the taxonomic response to fire was not matched by functional replacement.

4. These results suggest that greater functional stability to fire in the Mediterranean is achieved by replacement of functionally similar species (i.e. functional redundancy) which dominate under different environmental conditions in the heterogeneous landscapes of the region. In contrast, the greater functional response in the temperate region was atsctonm(ut(ed toa mofir)12.9(eer)7.1(a)21(id post- fir)1
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hoverflies; Greenleaf *et al.* 2007, bees), and nesting characteristics (Westrich 1989, bees). The response of birds and fishes to environmental changes has been assessed recently by considering a set of functional traits, allowing for the assessment of mechanisms regulating community assembly, species turnover and resilience (e.g. Mason *et al.* 2007; Petchey *et al.* 2007). For invertebrates, most efforts have focussed on identifying groups of organisms with similar ecological behaviours (e.g. Faber 1991). Belaoussoff *et al.* (2003) and Kevan *et al.* (1997), however, have highlighted the problem of defining functional groups for ground beetles and bees respectively. The concept of functional trait composition has been introduced to avoid arbitrary decisions about the level at which interspecific differences among species are functionally significant (Mason *et al.* 2005, Petchey & Gaston 2006; de Bello *et al.* 2007a; Díaz *et al.* 2007a).

In this study, we use bee community responses to fire as a model of animal functional trait response because these communities react rapidly and markedly to environmental changes (see Kevan 1999 for a review). Bees represent an important, and well-known, component of biodiversity that provides a wide range of goods and services to mankind (Díaz 2005; Kremen 2005) and contribute to the maintenance of terrestrial food webs and ecosystem function (Biesmeijer *et al.* 2006; Kremen *et al.* 2007). Their taxonomy is well known and the nomenclature is relatively stable (Westrich 1989). Fire is an important environmental driver worldwide and alters the structure and composition of the soil and vegetation which in turn dramatically affect bee communities through changes in resource distribution and habitat conditions (Reed *et al.* 2000).

While the taxonomical response of bees to fire have been assessed in different studies (Potts *et al.* 2003a,b, 2005b), generalizations beyond the specific locations have been limited as little is known of the functional response of bees to disturbance. As a group, bees exhibit a range of trait states which allow them to exploit of a wide range of habitats (Michener 2000; Greenleaf *et al.* 2007). The body size of these organisms is an important adaptation allowing larger species to exploit cooler thermal windows that are normally unavailable to smaller species (Willmer & Stone 2004). Similarly, in Argentina, social bee species were found to be better able to utilize small forest fragments than solitary species because of their ability to exploit them effectively through social foraging (Aizen & Feinsinger 1994). We therefore expect bee communities living in fire-prone regions to be dominated by large early-flying social generalists that are able profit from the post-fire conditions and use the mosaic of burnt and unburnt patches within a given area. However, little is known to what extent these expectations can be extrapolated to different regions and environmental conditions, and findings from studies looking at other organisms, such as plants, are controversial (Díaz, Noy-Meir & Cabido 2001).

In this context, the aim of our study is to compare the response of bees to fire in two ecosystems with contrasting climatic conditions (i.e. Mediterranean vs. temperate). We expect that comparing taxonomic and functional responses of bees to fire in two countries with different biogeographical and historical contexts would allow us to test to what extent the bees' response to fire can be generalized beyond distinct regions. We predict that: (i) fire affects both species and functional composition of bees at both taxonomic and functional levels, that is, through extinctions, immigrations, or dominance redistribution within the community; (ii) the response of bee communities to fire is smaller in the Mediterranean region because of the longer history of fire in arid conditions.

Methods

STUDY AREA

Bee data were collected in two study areas: (i) in the north of Israel ('Mediterranean region'), and (ii) in the south of Switzerland ('temperate region'). The Mediterranean sites were located in the Mount Carmel National Park (32°44′N, 35°00′E, 130–340 m a.s.l.), in an area of approximately 150 km^2. The vegetation is dominated by Aleppo pine (*Pinus halepensis*) woodland and various post-fire scrub habitats. The climate is characterized by hot dry summers and cool wet winters. Detailed descriptions of the study area can be found in Potts *et al.* (2003a,b). The temperate study sites were located in an area of uniform south-facing slopes (450–850 m a.s.l.) within a 165-km^2 area in the Locarno region, Switzerland (46°09′ N, 08°44′ E). The vegetation is dominated by stands of former coppice of European chestnut (*Castanea sativa*). The climate is mild with wet summers and relatively dry winters. Further details of the study area are given in Moretti *et al.* (2002).

In both sites, fires maintain a mosaic of areas with different post-fire ages and specific vegetation types (Table 1), which are considered to be of conservation importance according to the European Habitat Directive of 1992. The two regions are, however, characterized by different historical land-use patterns and fire management practices. The Mediterranean vegetation type (phrygana) is highly prone to ignition and the intensity and extent of fires are higher than in the temperate region. Fires occur principally during the hot dry season, that is, between June and October (Ne'eman & Trabaud 2000). In contrast, fires in the temperate region are fast-spreading surface fires of low-medium intensity, which occur during the winter dry period, coinciding with vegetation dormancy (December to April). The vegetation is dominated by coppice stools of chestnut, in which trees recover to a full canopy within 15–20 years of fire (Delarze, Caldelari & Hainnard 1992).

SAMPLING DESIGN AND SPECIES COLLECTION

In both regions, the sampling design was based on the approach of space-for-time substitution (i.e. chronosequences) (Pickett 1989). We chose 21 sites in which different times had elapsed since the last fire in each region (Table 1). Fire-history data were obtained in Switzerland from the National and regional wildfire data base and dendrochronological methods, and in Israel from the Mount Carmel National Reserve data base (Israel Nature and National Parks Protection Authority). We avoided pseudo-replications, by choosing, wherever possible, sites with similar fire regimes in different portions of each region (Potts *et al.* 2003a; Moretti, Duelli & Obrist 2006).

Bees were collected with widely used sampling methods appropriate for the particular vegetation and topographical conditions of the two study regions (Potts *et al.* 2005a). In Israel, bees were sampled using standardized observation transects. In each site, a random start point was selected and a linear 200-m transect was walked in a

Table 1. Study sites (n) in Israel and Switzerland. The sites are assigned to one of four categories based on broad vegetation types along the successional gradient of time elapsed since the last fire

		Israel		Switzerland	
Fire categories	Time since fire	$n = 21$	Mediterranean phrygana	$n = 21$	Temperate chestnut forest
Fresh burnt	≤ 2 years	6	Bare ground with a flush of annuals, height < 0·5 m	5	Bare soil, standing dead trees, luxuriant herb and scrub layer (DBH < 5 cm).
Intermediate	6–17 years	6	Perennials dominate, (especially woody Lamiaceae, *Cistus* spp. and Aleppo pine (*Pinus halepensis*) with some annuals. Scrub with a height up to 2 m	7	Dense chestnut (*Castanea sativa*) coppice stand with high number of dead young shoots (DBH 5–10 cm).
Mature	20–30 yrs	3	Pine dominates with an understorey of perennial shrubs	3	Mature coppice stand with dense canopy cover (DBH 15–20 cm).
Unburned	> 30 years	6	Canopy of pine with patches of perennial shrubs	6	Old coppice stand out of turn with dense canopy cover (DBH 20–30 cm).
Vascular plant diversity:					
Mean alpha diversity (±SD) per site			21·9 ± 16·1 higher at fresh burnt sites (P = 0·006)		19·0 ± 8·0 higher at fresh burnt sites (P = 0·101)
Gamma diversity (all sites)			135		95
Beta diversity (gamma/alpha)			6·4		5·0

DBH = Diameter at breast height. The diversity in vascular plants in each region is shown (gamma = the overall number of species sampled within each region; alpha = means no. of species per site per region (P value, together with its decrease with the time elapsed since last fire, i.e. with linear regressions; SD = standard deviation; beta expresses the heterogeneity in species diversity in the study region).

random direction over a 20-min period at 08·00, 11·00 and 14·00 h. Bees encountered within 1·5 m on either side of the observer were recorded. Five sets of replicate transects were made at each site and separated by regular intervals through the peak flower blooming and bee activity season (March–May) in 1999. Additional details of the sampling design can be found in Potts *et al.* (2003a).

In Switzerland, bees were sampled using window (interception) traps combined with yellow water-filled pans and placed 1·5 m above-ground; at each of the 21 sites, three window traps were installed (distance between sites *c.* 300 m). The traps were emptied weekly from March to September 1997. For further details, see Moretti, Obrist & Duelli (2004).

Practical considerations dictated the choice of different trapping methods in each region. In Switzerland, sites had relatively low bee densities and therefore netting would have been an ineffective method, whereas in Israel, water-filled pans would have simply dried out in the intense heat. A recent large-scale study covering different habitat types compared the relative effectiveness of different trapping methods (Westphal *et al.* 2008). Despite differences in methodologies, the studies have large temporal and spatial coverage of the target habitats and provide robust data sets representative of the actual communities in the study systems (Potts *et al.* 2003a; Moretti, Obrist & Duelli 2004).

SPECIES DIVERSITY AND COMPOSITION

For each site within a region, the mean number of species (species richness), number of individuals and the Simpson's index of species diversity were calculated. The Simpson index is defined as 1 minus Simpson dominance (SD = 1 – D) where:

$$D = \sum_{i=1}^{s} p_i^2 \qquad \text{eqn 1}$$

with S being the number of species in the community, and p_i the proportion of ith species in a sample (i.e. $p_i = N_i / N$ and $N = \sum N_i$, where N_i is the number of individuals of the ith species). The index was calculated after $\log_{10}$ transformation of the number of individuals of each species, to reduce the effect of extreme values and the higher abundance of dominant species individuals (de Bello *et al.* 2007a). The response of species richness, number of individuals and Simpson index to fire were analysed by separate linear regressions; the predictor was the exact number of years since the last fire (and not the categories used in Table 1 to describe the vegetation types).

Species composition response to fire in each region was assessed by using partial redundancy analysis (pRDA) because the length of the first axis of the detrended correspondence analysis (DCA) was < 2·5 (Lepš & Smilauer 2003). In the pRDA, the time since fire was introduced as the only explanatory variable, and other site factors (i.e. altitude, slopes, aspect) were entered as covariates to reduce noise in site variation that is not directly related to fire (Lepš & Smilauer 2003). Data were analysed using CANOCO for Windows version 4·5 (ter Braak & Šmilauer, 2002). Log_{10} transformation of the number of individuals was used to reduce the effects of extreme values and to make the two sampling methods more comparable. All species occurring only in one site per region were removed from the analyses, to exclude casual occurrences and avoid distortions in the analyses (Lepš & Smilauer 2003).

SPECIES TRAITS

All adult bees were identified to species, or morphospecies level for some unresolved bee genera (particularly in Israel, where appropriate keys are not available). Nomenclature follows Michener (2000) for family classification and Westrich (1989) for species nomenclature. Voucher specimens of each species are deposited in the Natural History Museum of Lugano, Switzerland and the University of Oxford Museum, UK. Each species was described in terms of 24 functional traits belonging to eight trait groups (Table 2). The selection of traits was based on characteristics that are recognized as important in bee autoecology (e.g. Westrich 1989; Michener 2000)

Table 2. Description of the bee functional traits and categories used in the study. Traits were described for each species according to published sources or researcher expertise (where published information for a particular species was not available). For each trait, we calculated a mean trait (*mT*) per site. The index of functional diversity (FD) was calculated for each trait or for each group of traits treated as dummy variables (e.g. nesting specialization)

Trait groups	Trait code	Categories
Habitat specialization	HabitatSp*	Generalist[a]; intermediate[b]; specialist[c]
Feeding strategy	FlowAc	Flower access: restricted to tubular flowers; both tubular and open flower types; open flowers
	FeedSp†	Feeding specialization: no lectic status[a]; polylectic[b]; oligolectic[c]; monolectic[d]
	TongL	Tongue length: short tongue; long tongue
Nesting specialization (NestSp)	NoNest	No nest building (i.e. cleptoparasitic)
	Miner	Excavator in the ground
	Carpent	Excavator in woody substrate
	Mason	Building nest with mud
	RentShel	Renter on the ground, particularly in snail shells
	RentAerial	Renter of pre-existing nest and holes above the ground
Parasitic status (Parasitic)	CleptoP	Cleptoparasitic (i.e. solitary parasitic bee)
	SocialP	Social parasitic
	NonParas	Nonparasitic
Social status	Social‡	Solitary[a]; variable[b]; social[c]
Pollen transport (dummy variables) (PolTransp)	AccidPol	Carried 'accidentally' on body
	Crop§	Carried internally in the crop
	OnLegs	On the legs
	LegsBody	On legs and body
	UAbdom	On the underside of abdomen
Flight phenology	FlyStart	Flight season start (month)
	FlyFinish	Flight season finish (month)
	FlyDurat	Mean flight duration (month)
	Voltinism	Number of generations per year: univoltine; bivoltine; multivoltine
Dispersion	ITD¶	Inter-tegula distance (μm)

*[a]Utilizing 1 habitat type; [b]utilizing 2–4 habitat types; [c]utilizing ≥ 5 habitat types; †[a]having no pollen collecting requirements (i.e. a cleptoparasite); [b]pollen collecting on a number of species from different plant families; [c]pollen collecting restricted to plants within the same plant family; [d]pollen collecting at a single species; ‡[a]solitary, communal and semi-social; [b]species is either solitary or social depending upon locality/environmental conditions; [c]colony founded by single individual on annual cycle (primitive eusocial) or a year-round colony (advanced eusocial); §defined morphologically after Michener (2000); ¶distance between the two insertion points (tegula) of the wings.

and among those that relate to different ecosystem processes (Biesmeijer *et al.* 2006; Fontaine *et al.* 2006). In all cases where morphospecies were used, traits were either consistent across all species within the genus or inferred from known traits of closely related species.

FUNCTIONAL TRAIT COMPOSITION

Functional trait composition was assessed using two approaches which are increasingly used in studies assessing functional composition of biotic communities (Díaz *et al.* 2007b; Mason *et al.* 2007; Petchey *et al.* 2007; Lavorel *et al.* 2008). First, the mean trait per community (*mT*) can be calculated for each trait as the average of trait values in the community, weighted by the relative abundance of the species carrying each value (see below). This metric is often understood as defining the dominant traits in a community. Second, the distribution of trait values within the community can be expressed through various metrics, among which functional diversity is increasingly used (Lepš *et al.* 2006; Petchey & Gaston 2006; Mason *et al.* 2007), and measures the degree of overlap in trait values within the community and reflects how the species share the available niche space (Mason *et al.* 2005).

These components were calculated for different traits and each site. The *mT* was calculated as an average for a given trait weighted by species abundance, according to Garnier *et al.* (2004), as:

$$mT = \sum_{i=1}^{s} p_i x_i \qquad \text{eqn 2}$$

where x_i is the trait value of ith species (for binary traits x_i can be either zero or one). The functional diversity (FD) was calculated, for different traits, on the basis of the Rao index of diversity (Rao 1982; Ricotta 2005; Lepš *et al.* 2006) as:

$$FD = \sum_{i=1}^{s} \sum_{j=1}^{s} d_{ij} p_i p_j \qquad \text{eqn 3}$$

where d_{ij} expresses the dissimilarity between each pair of species i and j. The FD index equals the sum of the dissimilarity in trait space among all possible pairs of species, weighted by the product of the species' relative abundance. The parameter d_{ij} varies from 0 (two species have exactly the same traits) and 1 (two species have completely different traits). For example, in the case of binary traits, when the species has the same trait value, then $d_{ij} = 0$; when they have different values, then $d_{ij} = 1$. In our case, all traits were treated as semi-quantitative variables and scaled between 0 and 1, including quantitative traits such as inter-tegula distance (ITD), to standardize trait dimensions (see Botta-Dukat 2005; Lepš *et al.* 2006; and http://botanika.bf.jcu.cz/suspa/FunctDiv.php to calculate FD).

Table 3. (a, b) Effect of fire regime on bee communities in the two climatic regions, that is, Mediterranean (Israel) and temperate (Switzerland). (a) Linear regressions between time since fire and the mean number of individuals, species richness and Simpson index of diversity per site ($n = 21$ within each region). For each regression, the beta coefficient, the R^2 of the model and the significance of predictors (in bold $P < 0{\cdot}05$ values) are shown. (b) Gradient analyses [i.e. DCA (detrended correspondence analysis) and pRDA (partial redundancy analysis), see Methods] to assess the effect of time since fire on species and functional composition (mean traits and functional diversity). The DCA indicates the total variability in the data set (total inertia). Each pRDA tests the effects of time since fire (Tfire), both as variance explained and significance. All the response variables (with the exception of the number of individuals and species richness) are based on $\log_{10}$-transformed abundance data

'Time since last fire' as explanatory variable	Mediterranean (no. of species = 115)			Temperate (no. of species = 145)		
a) Linear regression	Beta coeff.	R^2	*P* value	Beta coeff.	R^2	*P* value
Number of individuals	–0·041	0·123	NS	–0·207	0·183	0·052
Species richness	–0·127	0·195	**0·045**	–0·415	0·301	**0·010**
Simpson index of diversity	–0·001	0·023	NS	–0·001	0·318	**0·008**
b) Gradient analysis	DCA Total inertia	pRDA Tfire expl. var.	*P* value	DCA Total inertia	pRDA Tfire expl. var.	*P* value
Species composition	3·109	9·1%	**0·003**	0·531	11·7%	**< 0·001**
Mean trait composition ($n = 24$)	0·211	5·9%	0·322	0·022	22·4%	**< 0·001**
Functional diversity ($n = 13$)	0·075	5·7%	0·356	0·006	21·9%	**< 0·001**

The Rao index is a generalization of a Simpson index of diversity because if $d_{ij} = 1$ for any pair of species (i.e. each pair of species is completely different), then FD is equal to the Simpson index of diversity SD (1) (see Ricotta 2005 for details). In natural communities, however, the Simpson index and the Rao FD vary independently (de Bello, Lepš & Sebastià 2006; de Bello *et al.* 2007a), therefore the Rao index does not necessarily produce correlated indices of species and functional diversity (as, for example, Petchey *et al.* 2007). Compared to other indices of functional diversity, the Rao index includes information of species abundance, which is a relevant parameter modulating the effects of species and trait composition on several ecosystem processes (e.g. Petchey & Gaston 2006; Ricotta & Moretti 2008).

Following the calculation of mT and FD for the different traits and sites, we used pRDA to test the effect of fire on functional trait composition indices in each region. The pRDA was applied with the same approach used to assess the effect of fire on species composition (i.e. time since fire was the only explanatory variable and other site factors were covariates). As for species diversity and species composition, the number of individuals in the calculation of mT and FD was $\log_{10}$ transformed.

Results

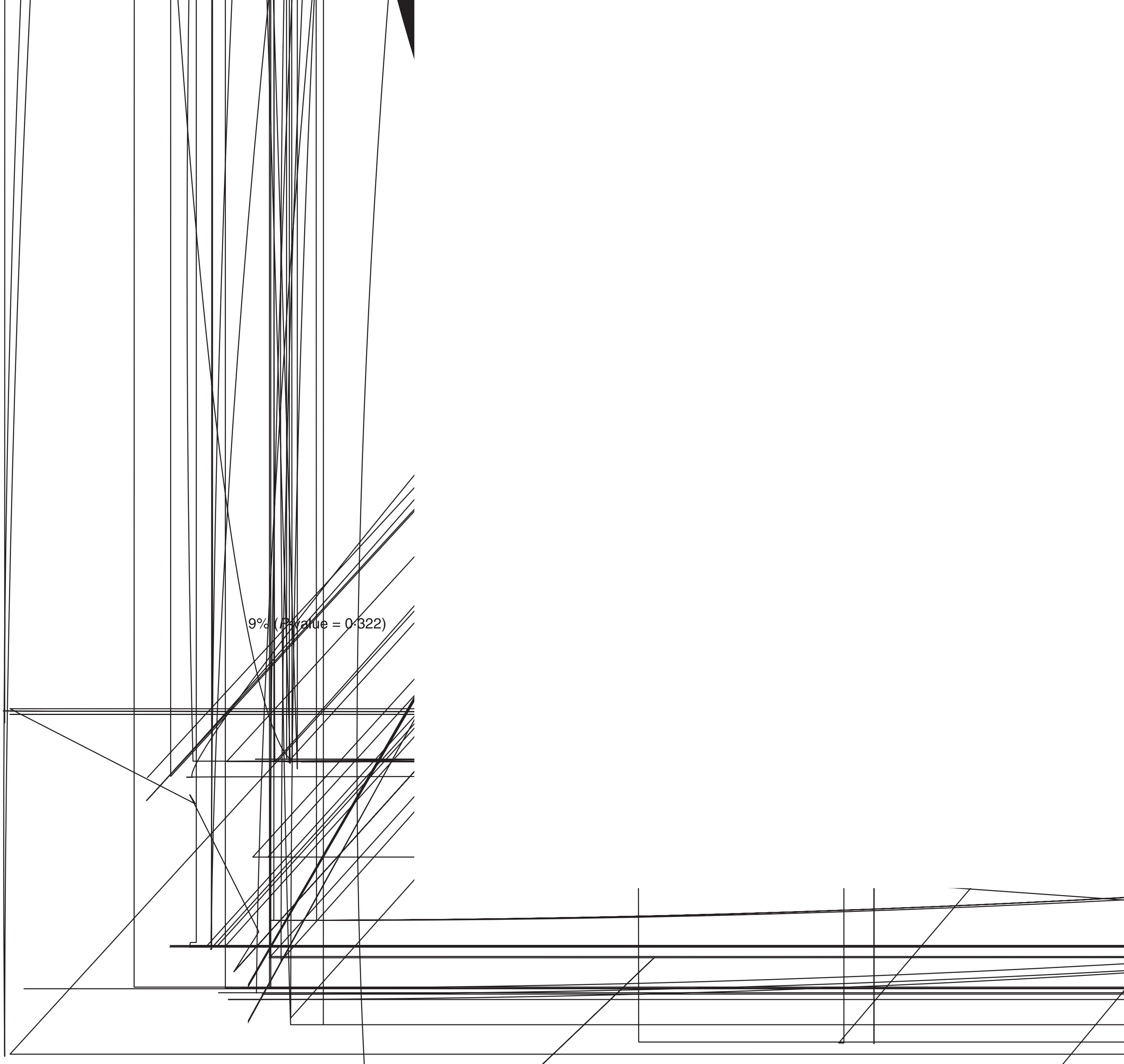
CHANGES IN SPECIES DIVERSITY AND COMPOSITION

The overall species composition differs markedly between the two countries. In Israel, 115 species were collected and 145 in Switzerland. Only 1·5% of the overall species were found in both Israel and Switzerland. In both countries, species richness declined with time elapsed since fire (Table 3, Appendix S1), but the decrease in species diversity and number of individuals was more marked in the temperate region (Table 3). Time since fire had a similar effect on species composition in both countries [Israel: pRDA, variance explained (var. expl.) 9·1%, $P = 0{\cdot}0034$; Switzerland: pRDA, var. expl. 11·7%, $P = 0{\cdot}0004$; Table 3]. However, the total variability in species composition was higher in the Mediterranean region (DCA total inertia, Table 3, Appendix S2).

About one-third (Israel) and up to half (Switzerland) of the dominant and subdominant species shifted in dominance along successional gradient in both countries (see Supporting Information Appendix S3). In Israel, the honeybee (*Apis mellifera*) was the most abundant species at fresh and intermediate burn sites (33% of individuals) and decreased in abundance in unburnt sites (20%), while *Lasioglossum marginatum* (21% in freshly burnt sites) became increasingly abundant at unburnt sites (36%) (see Appendix S3). In Switzerland, *Andrena minutula* was the most abundant species during all successional stages (18–44%). *Lasioglossum morio* was dominant during the two early post-fire stages (15–16%) and decreased gradually as succession proceeded (4–5%), while *A. mellifera*, a sub-dominant species immediately after the fire (8–9%), was dominant in the unburnt sites (26%) (see Appendix S3).

CHANGES IN TRAIT COMPOSITION AFTER FIRE

Fire explained a relatively small amount of variance in trait composition in Israel (mT: 5·9%, $P = 0{\cdot}322$; FD: 5·7%, $P = 0{\cdot}357$; Table 3) compared to Switzerland (mT: 22·4%, $P = 0{\cdot}0002$; FD: 21·9%, $P = 0{\cdot}0002$) (Table 3). In Switzerland, fire affected several traits in terms of both mean (mT) and functional diversity (FD) (see Fig. 1 and Table 4 for a synthesis). Freshly burnt sites were characterized by species that start and finish flying late in the season (+FlyStart$_{mT}$/FD; +FlyFinish$_{mT}$) and with more than one generation per year (+Voltinism$_{mT}$). Bees at freshly burnt sites were short-tongued (–TongL$_{mT}$/FD), solitary (–Sociality$_{mT}$/FD), low-dispersal species (–ITD$_{mT}$), displaying diverse modes of pollen transport, in particular internally in the crop (+Crop$_{mT}$/FD), and nesting specialization, with a high proportion of species excavating their nests in wood (+Carpenter$_{mT}$/FD) and nesting in existing cavities (+RentAerial$_{mT}$/FD). On the other hand, in Israel, fire induced only a small, but significant ($P < 0{\cdot}05$), shift in mT and FD, with a higher proportion of short dispersal (–ITD$_{mT}$) species nesting in snail shells (+RentShel$_{mT}$) and transporting pollen



$_{mT}$). Overall, the shift in trait
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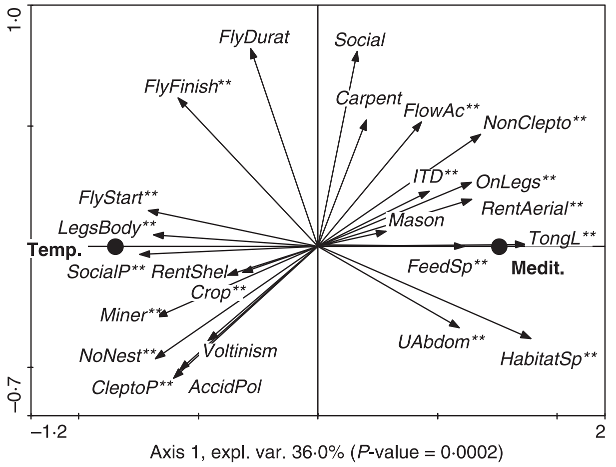
ed, $P = 0{\cdot}0002$; Fig. 2). In the
different strategies in feeding, nesting, and pollen transport, as well as distinct habitat specialization (see Table 4 for a synthesis) in terms of both mean trait (*mT*) and functional diversity (FD). Israeli bee communities were dominated by large (+ITD$_{mT/\mathrm{FD}}$), lectic specialists (+FeedSp$_{mT}$), mainly feeding on open flower corollas (+FlowAc$_{mT/\mathrm{FD}}$), while transporting pollen on the legs (+OnLegs$_{mT/\mathrm{FD}}$) and under the abdomen (+UAbdom$_{mT/\mathrm{FD}}$). Mediterranean bees mainly flew from early to late spring (–FlyStart$_{mT}$ and –FlyFinish$_{mT/\mathrm{FD}}$), and nested in existing cavities (+RentAerial$_{mT/\mathrm{FD}}$). Under temperate conditions in Switzerland, bees tended to be short-distance dispersers (–ITD$_{mT/\mathrm{FD}}$), solitary (–Social$_{\mathrm{FD}}$ + CleptoP$_{mT/\mathrm{FD}}$) generalists, with wide

(a) Mean traits (*mT*)



(b) Functional Diversity (FD)

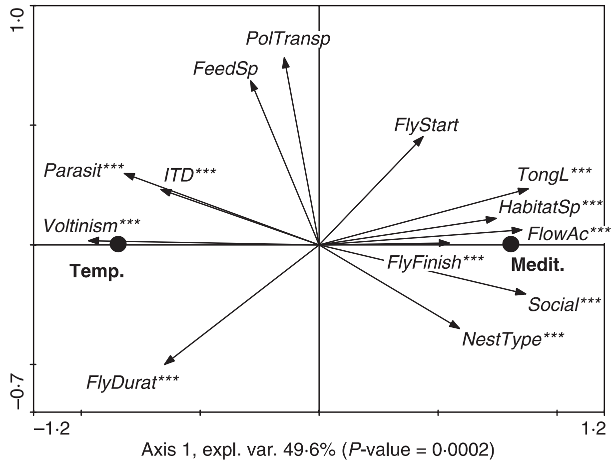


Fig. 2. (a, b) Changes in functional trait composition indices, that is, mean trait (a) and functional diversity (b), between the two study climatic regions (temperate vs. Mediterranean). Biplots of the partial redundancy analyses (pRDA) with region as an explanatory variable and fire as a covariable. *P* values from a Monte Carlo test of significance of the first axis (4999 iterations). For trait codes, see Table 2. The significance in the change for each trait (or trait groups for FD) is shown (GLM): *≤ 0·05; **≤ 0·01; ***≤ 0·001.

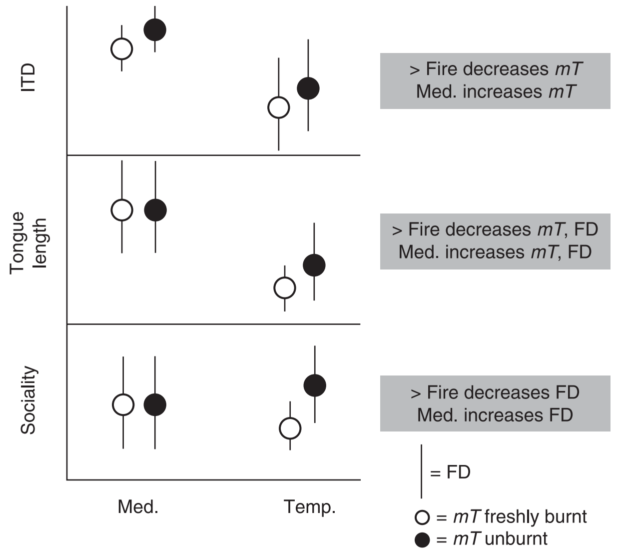


Fig. 3. Schematic examples of the 'divergent selection' by region [Mediterranean (Med) *vs.* temperate (Temp) region] and fire [freshly burnt (○) vs. unburnt (●) sites] on three traits (ITD, tongue length, and social status; see Table 2). High mean values (*mT*) of ITD and tongue length of bee communities are selected for in the Mediterranean (Med.) compared to the temperate (Temp) region, while freshly burnt sites (○) select for the opposite (lower) trait values (at least in one region) compared to unburnt sites (●). The functional diversity (FD, vertical bars) is higher in the Mediterranean region for tongue length and social status, while it is lower at freshly burnt sites.

habitat (–HabitatSp$_{mT/\mathrm{FD}}$) and feeding requirements (–FeedSp$_{mT}$), transporting pollen on both legs and body (+LegsBody$_{mT}$) and in the crop (+Crop$_{mT}$), and being active late in spring and summer (+FlyStart$_{mT}$; +FlyFinish$_{mT/\mathrm{FD}}$), or were cleptoparasites (+CleptoP$_{mT/\mathrm{FD}}$) (see Figs 2 and 3 for a visual representation).

Discussion

Our results show that bee communities respond both taxonomically and functionally to fire, but the patterns of these shifts differ between climatic regions (Mediterranean vs. temperate). Although the taxonomical response was similar in both regions, the functional response was more marked in the temperate region and more stable in the Mediterranean.

From the taxonomical point of view, the extent of the changes in species assemblages in Israel and Switzerland was generally consistent, which suggests that species rearrangement following disruption by fire, and progression of succession, produce similar effects in both regions. More species were observed at freshly burnt sites compared to the mature and unburnt sites. Consistent with other studies of ecosystems prone to disturbance (e.g. Bengtsson *et al.* 2000), the positive effect of fire on species diversity (see Supporting Information Appendix S1) and composition (Table 3) was mainly restricted to the early post-fire stages following changes in vegetation structure and diversity. The freshly burnt sites supported the highest floral diversity (Table 1), and so were likely to provide the widest range of resources for bees (Potts *et al.* 2003a). During post-fire successional stages (i.e. 6–17 and 20–30 years after the fire), a quick recovery of vegetation with a decrease of flower diversity might have driven bee diversity to pre-fire levels, as is often observed for other flower-feeding insects in ecosystems prone to disturbance (Force 1981; Swengel 2001).

Functional traits selected by fire were very similar in both countries, with fire consistently selecting for short-tongued low-mobility species which start flying later in the season. However, we also identified different patterns in response to fire in the two regions for some traits (e.g. social status, pollen transport and voltinism; Table 4). For example, we expected a major role to be played by fire in driving nesting resources and therefore structuring the bee community in both countries (Cane 1991; Potts *et al.* 2003a, 2005b). Our results, however, showed that fire affected nesting strategies in Switzerland only. The positive association between excavator bees in

Table 4. Schematic summary of the results of the study (see Figs 1 and 2 for details). Response of trait composition indices of bees (i.e. mean trait, *mT* and functional diversity, FD) to time since fire (young, freshly burnt sites vs. old, unburnt sites) within each climatic region (Mediterranean and temperate) and to climate (i.e. between-region effects after having removed fire effect, Mediterranean vs. temperate) calculated with multivariate analyses (pRDA; see methods)

		Time since last fire (young *vs.* old)				Climatic region		
		Mediterranean (Israel)		Temperate (Switzerland)		Mediterranean *vs.* Temperate		Trait selection on *mT* and FD by freshly burnt sites *vs.* Mediterranean
Trait groups	Traits	*mT* Fig.1a	FD Fig.1c	*mT* Fig.1b	FD Fig.1d	*mT* Fig.2a	FD Fig.2b	
Habitat specialization	HabitatSp	NS	NS	NS	NS	+ Med	+Med	–
Feeding strategy	FlowAc	NS	NS	NS	NS	+Med	+Med	Divergent (mT, FD)
	FeedSp	NS	NS	NS	NS	+Med	NS	
	TongL	NS	NS	+old	+old	+Med	+Med	
Nesting specialization	NoNest	NS	NS	NS	+young	+Temp	+Med	Convergent (mT, FD)
	Miner	NS		+old		+Temp		
	Carpenter	NS		+young		NS		
	Mason	NS		NS		NS		
	RentShel	(+young)		NS		NS		
	RentAerial	NS		+young		+Med		
Parasitic status	CleptoP	NS	NS	NS	NS	+Temp	+Temp	–
	SocialP	NS		NS		+Temp		
	NonClept	NS		NS		+Med		
Social status	Social	NS	+old	+old	+old	NS	+Med	Divergent (FD)
Pollen transport	Crop	NS	NS	+young	+young	+Temp	+Med	Divergent (*mT*, FD)
	OnLegs	NS		+old		+Med		
	LegsBody	NS		NS		+Temp		
	UAbdom	(+young)		NS		+Med		
Flight phenology	FlyStart	NS	NS	+young	+young	+Temp	NS	Divergent (*mT*, FD)
	FlyFinish	NS	NS	+young	+old	+Temp	+Med	
	FlyDurat	NS	NS	NS	NS	NS	+Temp	
	Voltinism	NS	NS	+young	NS	NS	+Temp	
Dispersion	ITD	(+old)	NS	+old	NS	+Med	+Temp	Divergent (*mT*)

For trait indices responding significantly to environmental factors (linear regression and GLM with $P < 0{\cdot}05$), the direction of change is indicated (i.e. +young = increase at freshly burnt sites; +old = increase at unburnt sites; +Med or +Temp = increase in the Mediterranean or temperate region; in brackets = near to significance, i.e. $0{\cdot}05 < P < 0{\cdot}1$; NS = nonsignificant). For example, the mean tongue length (TongL) of the bee community is longer and a more diverse trait in the Mediterranean (+Med) and in old fire sites (unburnt) in temperate forests (+old). For trait codes, see Table 2. Traits related to nesting specialization (6 traits), pollen transport (6 traits), and parasitic status (3 traits) have been treated as dummy variables (i.e. one FD value per trait group was calculated). The last column indicates the selection effect produced by fire vs. climatic region (i.e. freshly burnt sites vs. Mediterranean): 'Convergent' is defined as an increase of *mT* and/or FD at both freshly burnt sites and Mediterranean region (i.e. +young/+Med as for 'RentAreal' or, vice versa +old/+Temp as for 'Miner'). 'Divergent' is the opposite pattern (i.e. +young/+Temp or, vice versa +old/+Med as for most traits). For a schematic representation of divergence, see Fig. 3.

woody substrate (carpenters, e.g. *Xylocopa* spp. and *Ceratina* spp.), renters of pre-existing holes (aerial renters, e.g. *Hylaeus* spp. and *Osmia* spp.) and the recent fires in Switzerland, confirm our expectation that fresh and intermediate burnt sites provide suitable nesting conditions in damaged and dead wood. This appears to be true in the low-intensity burn in temperate forests, while the more intensive fires in the Mediterranean are associated with the combustion of stems and twigs suitable for aerial nesters with only large trunks remaining post-fire.

The different patterns of bee trait responses to fire in the two regions highlight the contemporary selection of regional conditions (i.e. climate, vegetation type etc.) and fire regime on the functional component of the communities and regional species pool. We observed a strong differentiation in the bee traits between the two regions (Table 4 and Fig. 2), which were also contemporarily affected by fire regime (Fig. 3). Therefore, the different functional response can be explained by the different regional trait pools from which communities rebuild after fire. According to Potts *et al.* (2003a,b), unburnt and mature sites in Israel tend to have a greater coverage of plants which produce flowers with high nectar volumes and long corollas only accessible to large and long-tongued bees (e.g. Apidae, and large Megachilidae) that can start flying earlier in the season (March–April). Temperate regions are, on the other hand, mainly dominated by small bees, which are generally warmth-demanding species and thus start flying later in the season (May–June) when it is warmer. Therefore, the response of traits, such as body size and flight season, might have been affected by both regional conditions and fire regime showing that traits responding to a specific disturbance regime cannot be simply generalized across regions.

Overall, our results show a more marked response of mean traits (*mT*) and FD to fire in the Swiss temperate forests compared to the Mediterranean habitats (Table 3, Fig. 1). This suggests a lower functional redundancy in response to environmental change (Petchey *et al.* 2007) in Switzerland and a lower functional trait shifts (higher redundancy) of bee in the Mediterranean. This confirms the expectations of higher stability towards perturbation (i.e. high resistance and resilience to disturbance) under more severe evolutionary selection by fire in the Mediterranean region. Interestingly, our results give insights into the mechanisms of this higher redundancy. For example, we found consistent and frequent evidence that Mediterranean environmental conditions and fire regime can have a divergent effect on similar traits (*sensu* McDonal *et al.* 2003, i.e. for a given traits, two environmental factors select for opposite trait states), as shown for tongue length, inter-tegular distances, and bee social status (see Table 4 and Fig. 3). For instance, bees dominant in the Mediterranean (i.e. under severe summer climatic conditions) have longer tongues and inter-tegular distances and so do the bees occurring at unburned sites in Switzerland (i.e. fresh conditions). Similarly, higher diversity in social status was observed in the Mediterranean and unburnt sites in both climatic regions. As a result of this divergent selection, FD is often higher under Mediterranean conditions. In fact, despite the higher number of species sampled in the temperate region, 7 out of 11 traits that responded to climatic conditions showed a higher FD in the Mediterranean region (Table 4). Indeed there was a higher inertia value among both the species and trait composition gradients in Israel than in Switzerland (DCA, Table 3), suggesting that the Mediterranean bee community has a higher heterogeneity in species and trait assemblage, which is not determined only by fire. In the Israeli phrygana, as in many Mediterranean ecosystems, high habitat heterogeneity is maintained by a long fire history and co-existence of different land uses more generally (e.g. Grove & Rackham 2001). A higher alpha and beta plant diversity in Israel, compared to Switzerland (Table 1), is consistent with the higher heterogeneity in plant composition in the Mediterranean landscapes compared with temperate ones (e.g. de Bello, Lepš & Sebastià 2007b). Such landscape and resource mosaics can be easily exploited by the larger bees that dominated the communities in Israel. In the Swiss temperate forests, the strong re-growth vigour of the sweet chestnut coppice drives the post-fire succession (e.g. Delarze *et al.* 1992). This reduces the time-window when favourable post-fire habitat is available for bees, therefore reducing the heterogeneity in bee species and trait assemblage as indicated by the low species and trait inertia (DCA, Table 3).

The higher heterogeneity in bee traits in the Mediterranean (high FD) appears to allow a more stable functional community rebuilding after fire, as shown by a low functional response towards disturbance in functionally diverse plant communities (Walker, Kinzig & Langridge 1999). According to these authors, functional stability towards disturbance might be maintained by replacement of functionally similar species, which dominate under different environmental conditions. This process is enhanced by high local FD, since more strategies and niches are available in the pool that can be interchanged, determining a shift in species composition but not in functional assemblage (as defined by Petchey *et al.* 2007 as ecological redundancy). Therefore, the interaction between perturbation factors and the environmental matrix of the surroundings combine to shape the different mechanisms of community responses to fire.

Conclusions

Our results show that species and bee trait responses to fire are not exclusively the result of the fire regime, but rather of a combination of factors, including the climate, historical aspects (mainly land use) and landscape structure. This suggests that using traits to predict the response of communities to environmental changes and habitat contexts should be considered when interpreting bee community responses to disturbance. Extrapolations based on simple species traits cannot be generalized to all conditions and should be applicable only within comparable situations. Furthermore, despite the significant shift in species composition with fire in the Mediterranean and temperate regions, functional composition parameters remain more stable in response to fire in the Mediterranean. Such stability seems to be regulated by the region characteristic functional composition and higher diversity in traits in the system.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Summary of species richness (number of bee species; Fisher alpha diversity), Simpson diversity and number of individuals sampled for each fire age category for Israel and Switzerland (Mediterranean vs. temperate regions)

Appendix S2. Partial redundancy analyses (pRDA) of bee species response to fire for the 21 sites in the (a) Mediterranean (Israel) and (b) temperate (Switzerland) regions (using time since fire as a variable and site factors as covariables)

Appendix S3. Bee composition changes with fire in the (a) Mediterranean and (b) temperate region