Co-occurrence of three *Aristolochia*-feeding Papilionids (*Archon apollinus*, *Zerynthia polyxena* and *Zerynthia cerisy*) in Greek Thrace

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Comparative studies of co-occurring species using overlapping resources may help in understanding the mechanisms supporting biotic diversity in species-rich regions, such as the Mediterranean region of Europe. Three Papilionidae butterflies, *Archon apollinus*, *Zerynthia cerisy* and *Zerynthia polyxena*, develop on *Aristolochia* plants and co-occur in Greek Thrace. We used mark–recapture to describe adult demography and dispersal, and searched for eggs and larvae to assess host plants and microhabitat preferences. Adult flight timing followed a sequence from earliest *A. apollinus*, through *Z. polyxena* to late *Z. cerisy*; this was more prominent in 2010 (warm early spring) than in 2011 (cold delayed spring). Population densities were highest for *A. apollinus* and lowest for *Z. cerisy*, whereas dispersal ability followed a reverse pattern. Adults of all three species crossed distances > 3 km and used all habitat types present. Four *Aristolochia* host plants were used at the study locality: small *Aristolochia pallida*, intermediate *Aristolochia rotunda* and *Aristolochia hirta*, and bulky, late-sprouting *Aristolochia clematitis*. Both *A. apollinus* and *Z. polyxena* used all four *Aristolochia* species, the former preferring *Aristolochia rotunda* and *Aristolochia hirta*, the latter *Aristolochia rotunda* and *Aristolochia pallida*. *Zerynthia cerisy* did not use the early-growing *Aristolochia pallida* while frequently using the late-growing *Aristolochia clematitis*. Further parameters affecting oviposition were biotope and canopy closure: early *A. apollinus* tolerated shady sites but late *Z. cerisy* avoided them. The simultaneous use of several host plants differing in phenology and habitat requirements, combined with rather high dispersal ability, arguably buffers the butterflies’ population dynamics against yearly variation in weather, while allowing efficient occupation of the diverse Mediterranean landscapes. The regional habitat diversity, created during millennia of human activity, is currently threatened by land abandonment, which may diminish the resource base for the studied butterflies.

**Keywords:** butterfly demography; dispersal; oviposition; Lepidoptera; Mediterranean region; phenology

**Introduction**

The Mediterranean Basin located at the conjunction of Europe, North Africa and western Asia represents one of the global biodiversity hotspots (Myers et al. 2000). Its biotic richness is determined by steep bioclimatic gradients, a long unglaciated history, and millennia of coexistence with humans, whose activity has contributed...
to the maintenance of diverse habitats (Grove and Rackham 2003; Mazzoleni et al. 2004; Blondel et al. 2010). Currently, Mediterranean landscapes are under interwoven threats of land-use intensification (including urbanization and coastal development) and abandonment (depopulation of remote areas, successional loss of open biotopes) (Debussche et al. 1999; Mazzoleni et al. 2004).

The processes that maintain Mediterranean biodiversity remain little studied, especially if compared with more northerly parts of Europe. This is well illustrated using the model group of butterflies. Although over two-thirds of European butterflies occur in Mediterranean states (cf. Kudrna et al. 2011), only a handful of papers have focused on this region. Apart of studies describing macro-scale patterns (e.g. Hortal et al. 2004; Fattorini 2006), analysing existing threats (e.g. Bonelli et al. 2011), or comparing effects of land uses (e.g. Grill and Cleary 2003; Grill et al. 2005; Kati et al. 2012), only a few studies have targeted the mechanistic details of species occurrence (e.g. Celik 2012; Verovnik et al. 2013). One approach to studying the mechanisms that maintain biodiversity is to compare life histories of sympatric related species overlapping in resource use. Such species may theoretically compete with each other (Thomas and Elmes 2001; Kunte 2008), unless they use different spatiotemporal niches. Alternatively, their resources may be sufficiently abundant to mitigate competitive interactions (e.g. Kalapanida and Petrakis 2012), or varied responses to abiotic factors may generate mutually independent population dynamics (WallisDeVries et al. 2011).

Middle-sized papilionid butterflies developing on birthworts (Aristolochia spp.) represent a guild of related, locally coexisting butterflies. Aristolochiaceae, the ancestral host plants of Papilionidae (Condamine et al. 2013), synthesize aristolochic acids, used by the butterflies both as oviposition clues and chemical protection (Klitzke and Brown 2000; Mebs and Schneider 2002). Seven Aristolochia-feeding papilionids occur in the Mediterranean (Tolman and Lewington 2009; Dapporto 2010). They overlap in host plants spectra (cf. Tolman and Lewington 2009), but little is known regarding details of their host preferences. Within Europe, the highest diversity of those butterflies is found in Greek Thrace, where three species co-occur (cf. Kudrna et al. 2011). Zerynthia polyxena (Denis and Schiffermüller, 1775) and Zerynthia cerisy are native to the region, whereas Archon apollinus was transferred there from European Turkey in the 1920s (cf. Tolman and Lewington 2009).

For two seasons, we studied the immature and adult habitat use of the three species in Greek Thrace, to elucidate their coexistence patterns. Here, we report our findings on adult demography, larval and adult phenology, and larval and adult distribution within a heterogeneous semi-cultural landscape, asking the following questions. (1) Do adults of the three species differ in their use of individual biotope types in the study area? (2) Do the three species differ in adult demography parameters, including population density, and are these parameters related to adult mobility? (3) How do immature of the three species use available host plants, are there discernible differences related to plant species, conditions or microhabitat? Based on these questions, we argue that the sympatric coexistence of the three species is mediated via sequential phenology of their host plants, plus by ability of all three species to use the diverse habitat mosaic at the study locality. As one of the three studied species, Z. polyxena, also enjoys legal protection in the EU, we briefly discuss the management implications of our findings.
Material and methods

Study area

Greek Thrace, i.e. the administrative provinces Alexandroupoli, Komotini and Xanthi, is situated on the southern slopes of the eastern Rhodope Mountains facing the Aegean coast in the south and open to penetration by eastern faunal elements, it represents a crossroads of three bioregions, Black Sea, Continental and Mediterranean (EEA 2012).

Our study locality (Figure 1) (40°58’ N, 25°50’ E; altitude 150–200 m; total area 95 ha) consisted of three stream valleys covered by ancient and partly abandoned cultural landscape near a once important and now almost depopulated village. Abandoned fields, alluvial grasslands, scrubs overgrowing former pastures, gallery groves along creeks and closed woods on steep slopes form a diverse vegetation mosaic (Figure 2j). The bedrock is acidic igneous intrusions overtopped by alkali sediments. The vegetation is submediterranean, with woody plants represented, e.g. by Juniperus oxycedrus, Pyrus amygdaliformis and Quercus coccifera in scrubby macchia, Platamus orientalis along the creeks, and Quercus pubescens and Carpinus orientalis in woodlands.

Study species

Archon apollinus (Figure 2a) is distributed from European Turkey and the Aegean islands through southern Turkey to Iraq, Syria, Jordan, Israel and Lebanon (Hesselbarth et al. 1995). It was released to Greek Thrace in 1918 and 1919, from stock originally from the Kuru Dagi Mountains, Turkey, 80 km to the east (Tolman and Lewington 2009). Of multiple Aristolochia host species reported in literature (Buresch 1915; Koçak 1982; De Freina 1985; Fuchs 1995), Aristolochia pallida (Figure 2d), Aristolochia hirta (Figure 2g), Aristolochia rotunda (Figure 2e) and Aristolochia clematitis (Figure 2f) occur in Greek Thrace.

Zerynthia cerisy (Figure 2b) occurs from the southeastern Balkan Peninsula through Turkey and Syria to Jordan, Lebanon and Israel (Hesselbarth et al. 1995). Its habitats range from dry grasslands to open woodlands, depending on the supply of Aristolochia host plants. Out of 16 potential hosts reported in literature (Hesselbarth et al. 1995; Tolman and Lewington 2009), in addition to those four mentioned above, Aristolochia sempervirens and Aristolochia parvifolia occur in Greek Thrace.

Zerynthia polyxena (Figure 2c)) is distributed from southeastern France through northern Italy, the Balkan Peninsula and northern Turkey to Kazakhstan, reaching southern Central Europe in the north (Kudrna et al. 2011; Zinetti et al. 2013). The habitat range is again wide (cf. Celik 2012). Out of the seven literature-reported Aristolochia host plants (Hesselbarth et al. 1995; Tolman and Lewington 2009), Aristolochia clematitidis, Aristolochia rotunda, Aristolochia hirta and Aristolochia pallida occur in Greek Thrace.

All the study species are univoltine, they overwinter as pupae and emerge in spring, their females lay eggs in small batches. In Greece, A. apollinus is the earliest-flying species (March to April on mainland) followed by Z. polyxena and Z. cerisy (late March to early July) (Pamperis 1997).
Figure 1. Position of the study area in northeastern Greece (dark dot on the map) and mutual positions of the three study subsites, with the mosaics of individual biotopes. The longest single moves of three study species: Aa, *Archon apollinus*; Zc, *Zerynthia cerisy*; Zp, *Zerynthia polyxena*.
Mark–recapture

We used mark–recapture to investigate adult demography, marking the butterflies in April–May 2010 (1267 captures over 26 marking days) and 2011 (1596 captures over 29 days). We based the markings on three stream valleys (Figure 1), each encompassing a mosaic of four main land-cover types: scrub (18 ha in total), open woodland (23 ha), close woodland (18 ha) and arable field (13 ha).

On each day with suitable weather (low wind speed, little cloud and air temperature > 14°C) one person marked the butterflies within each valley, paying even attention to the four main land-cover types and capturing as many butterflies of all three species as possible. Captured butterflies were marked with numbers using a waterproof pen and immediately released. For each (re)capture, we recorded the species, the code, sex, date and time (closest hour), habitat type and activity before capture [flying, chasing, patrolling, egg-laying, mating, resting (including basking), nectaring]. In 2011, we also recorded GPS coordinates of each capture event (Garmin GPSmap 60 C with precision of ±3 m).
**Comparison of adult activity patterns**

Log-linear models, computed in R (The R Core Team 2012) were used to compare the activity before captures with respect to habitat, sex and species. We first defined the null model with activity classes as dependent variable, and then used the information-theory approach Akaike information criterion (AIC) to select the most parsimonious model explaining the activity according to the variables species, sex, biotope and all their interactions.

**Adult demography and dispersal**

Demography parameters were estimated using the POPAN parameterization of the Jolly–Seber approach for open populations with time-varying deaths and recruitment in MARK (White 1999). The three estimated primary parameters are daily residence rates $\phi_i$ (which combines mortality and emigration), daily catchability $p_i$ and daily recruitment (the percentage entering the population) $pent_i$. Derived parameters include daily population size, $N_i$, and total population $N$. The primary parameters may be constant in time and sex ($.$), sex-dependent ($g$), time-dependent in a factorial ($t$), linear ($T$), quadratic ($T^2$) or cubic ($T^3$) manners. Time and sex can have additive ($g + t$, $g + T$, $g + T^2$…) or interactive ($g \times t$, $g \times T$, $g \times T^2$…) effects. The best-fitting models are selected from a range of candidate models according to the quasi-Akaike information criterion (qAIC) (Schtickzelle et al. 2002). Average residences were obtained from the best-fitting candidate model containing time-invariant $\phi_{avg}$.

Average longevity was obtained as $-\ln(\phi_{avg})^{-1}$.

To compare dispersal distances with respect to species and sex, we fitted the 2011 movements data for all individuals recaptured at least once using the inverse power function (IPF), estimating the probabilities ($p$) of movements to distance ($D$) (Hill et al. 1996; Baguette 2003), as, $p_{IPF} = a D^{-n}$. The parameters $a$ and $n$ were estimated by regressing the natural logarithms of the inverse cumulative proportions of individuals crossing 100-m classes (ln$p$) on the natural logarithms of distance (in km), i.e. $\ln(p) = \ln(a) - n\ln(D)$. We followed Zar (2009) to compare the slopes of the resulting regression functions.

**Eggs and larvae search**

Direct comparison of egg placements and larval distributions was complicated by the sequential phenology of the three butterflies and their host plants. To overcome this complication, we surveyed the developmental stages twice, early in April (egg-laying period), and early in May (larval period). We did so in the same sites where the mark–recapture was carried out.

From 4 to 10 April 2010, we searched for eggs on as many *Aristolochia* spp. plants as possible (Table 1). For each plant, we recorded habitat, plant species, its phenology (ranked variable: 1, unfolded leaves; 2, folded leaves, but not flowering; 3, flowering; 4, overblown, fruiting); butterfly species, egg number; egg placement (three categories: stalk, ventral leaf side, dorsal leaf side); plant sun exposure [ranked: 1, exposed in short ($\leq 0.3$ m) vegetation; 2, in scrub mantle or taller herbaceous vegetation; 3, under a scrub]; number of *Aristolochia* stems in surrounding 1 m (a1 m); proportion of laid/unlaid *Aristolochia* plants (laid/unlaid plants). We also recorded the covers of forbs and
Table 1. Phenology of the studied butterflies and their host plants, according to literature: Strid and Tan (1997), Carbonell (1991), Hesselbarth et al. (1995), Tolman and Lewington (2009).

| Flying period/ Efflorescence | Altitude (m) | Maximal annual stem height (cm) | March | April | May | June | July | August |
|-----------------------------|--------------|---------------------------------|-------|-------|-----|------|------|--------|
| Butterflies                 |              |                                 |       |       |     |      |      |        |
| *Archon apollinus*          | 0–1100       |                                 |       |       |     |      |      |        |
| *Zerynthia cerisy*          | 0–1000       |                                 |       |       |     |      |      |        |
| *Zerynthia polyxena*        | 0–900        |                                 |       |       |     |      |      |        |
| Plants                      |              |                                 |       |       |     |      |      |        |
| *Aristolochia clematitis*   | 0–1000       | 100                             |       |       |     |      |      |        |
| *Aristolochia hirta*        | 0–1000       | 60                              |       |       |     |      |      |        |
| *Aristolochia pallida*      | 400–1200     | 50                              |       |       |     |      |      |        |
| *Aristolochia rotunda*      | 0–1150       | 100                             |       |       |     |      |      |        |
grasses in 1-m and 5-m diameter circles around the focal plant (forb1 m, grass1 m, forb5 m, grass5 m); and covers of scrubs and trees in 10-m diameters (scrub10 m, trees10 m). We labelled each plant that had a positive eggs record with a numbered flag for a subsequent search for larvae. We recorded the same variables for a high number \((n = 686)\) of Aristolochia plants not bearing any eggs.

From 3 to 16 May, 2010, we located 85% of the previously labelled egg-bearing plants, searching for butterfly larvae, and searched at further randomly selected plants. If the larvae were found, we recorded their number (larvae number), butterfly species and instar. As for the eggs search, we counted Aristolochia species in a 1-m diameter circle \((a1 \ m)\) and focal plant phenology. Further, we estimated the number of Aristolochia leaves in a 1-m diameter circle \((leafl \ m)\). We also recorded a number \((n = 39)\) of Aristolochia plants without any butterfly species.

### Analysing egg and larval distribution

We applied general linear models in R, following four complementary approaches.

For the eggs (April data), we first asked, which predictors related to the host plant and its surroundings influenced egg placement. Separately for each species, we defined a binomial distribution model with logit link function, contrasting plants bearing eggs of the focal species against plants either bearing eggs of the other two species, or not bearing eggs at all (eggs of a species present versus absent). We first computed single-predictor models for all potential predictors, and then considered interactions between plant species, habitat and phenology. Finally, we constructed a multiple regression model, based on forward selection of predictors, including two-way interactions.

For the eggs, we also compared the preferences of the three species based only on positive eggs records, i.e. working only with plants bearing eggs, but adding the information on egg batch sizes. We first defined a model explaining the number of eggs per batch by butterfly species (Poisson distribution of errors). To this model, we sequentially added one-way interactions with potential predictors, so asking how were the between-species differences in numbers of eggs related to such predictors as plant species or habitat, and we again constructed a multiple regression model based on forward selection of predictors.

Analogous to eggs, we compared separately for each species, plants bearing larvae of the respective species against those bearing larvae of the other two species or not bearing larvae at all (larvae of a species present versus absent), using binomial distribution and logit link. We again started with one-way regressions, and proceeded towards the final model-based forward selection from all nominally significant predictors and two-way interactions.

Finally, we compared the larval counts of the three species, based only on plants with positive records but adding the information on larval group sizes, proceeding analogously to models with egg counts.

### Results

#### Adult activity, demography and dispersal

In 2010, only A. apollinus and Z. cerisy males were marked with sufficient intensity for reliable demographic estimates, whereas in 2011 the demography of all three species could be directly compared (Table 2).
Archon apollinus adults were active from early mornings, staying at sun-exposed spots while shady vegetation was still under hoar-frost. Zerynthia cerisy and Z. polyxena appeared later in the day, apparently requiring more sunshine for activity; the highest Z. cerisy flight was from noon onwards. Both A. apollinus and Z. polyxena were often chased from lower vegetation strata, whereas Z. cerisy frequently flew higher, overflying taller bushes and trees. When chased from a shady spot, all three species sought a sunny patch for basking.

The log-linear model for adult activity, based on captures from the year 2011, contained all factors of interest (i.e. habitat, sex and activity), plus all two-way interactions (e.g. species*sex, species*habitat, species*activity, habitat*activity, habitat*sex and activity*sex) (Null model: df = 143, deviance = 3959, AIC = 4348; fitted model: df = 52, 91, deviance = 90.79, AIC = 584.5). The interaction terms revealed, first, that although male captures prevailed in all species, relatively more females were captured in Z. polyxena (32%) than in Z. cerisy (23%) and A. apollinus (18%). More Z. cerisy captures originated from open woodland (58%), whereas the other two species were captured in similar proportions (30–40%) in open woodland and scrub. Archon apollinus patrolled more frequently (30%) than the remaining two species (~20%); Z. cerisy displayed direct flight more frequently (59%) than the other two species (~20%); and Z. polyxena was encountered while resting more frequently (40% versus A. apollinus: 29%, Z. cerisy 9%). Patrolling was most frequent in scrub (34%), followed by open woodland (28%) and close forest (17%). Resting was frequent in close forest (41%), followed by fields (31%). Oviposition was most frequent in close forest (9%) and more females were encountered in close forest (40%), than elsewhere (~20% in all habitats).

Modelled demography parameters (Table 3) showed that residence rates were higher for males in all three species, and higher for A. apollinus than for the remaining two species. Capture probabilities $p$ always factorially depended on marking day,
Table 3. Summary of best-supported Jolly–Seber models (bold) and models with time-invariant residence, used to estimate demographic parameters and population sizes of *Archon apollinus*, *Zerynthia cerisy* and *Zerynthia polyxena* in Greek Thrace, 2010 and 2011, plus the respective estimated numbers of individuals, average residence times and maximum residences observed.

| Butterfly species | Model | AIC | Δ AIC | No. of parameters | Estimated males (± SE) | Estimated females (± SE) | Average residence time M/F | Maximum residence observed M/F |
|-------------------|-------|-----|-------|-------------------|------------------------|--------------------------|---------------------------|-----------------------------|
| *A. apollinus*, 2010 | \( \varphi (g + t) p (g + t) \) \( \text{pent} (g + T^2) N (g) \) | 3022.1 | 0 | 34 | 1326 (±122) | 1327 (±122) | 6.1/6.1 | 14/8 |
| | \( \varphi (g) p (g + t) \) \( \text{pent} (g + T^2) N (g) \) | 3027.9 | 5.8 | 22 | 1330 (±64) | 1331 (±64) | | |
| *A. apollinus*, 2011 | \( \varphi (g) p (g + t) \) \( \text{pent} (g + T^2) N (g) \) | 3516.6 | 0 | 34 | 992 (±48) | 707 (±96) | 8.2/4.5 | 28/14 |
| | \( \varphi (g) p (g + t) \) \( \text{pent} (g T^2) N (g) \) | 3521.7 | 5.1 | 36 | 976 (±49) | 672 (±86) | | |
| *Z. cerisy*, 2010 | \( \varphi (.) \) \( t \) \( \text{pent} (T) N (g) \) | 382.2 | 0 | 16 | 166 (±31) | – | 4.7/– | 12/– |
| | \( \varphi (.) \) \( t \) \( \text{pent} (T^2) N (g) \) | 384.4 | 2.2 | 17 | 176 (±27) | – | – | – |
| *Z. cerisy*, 2011 | \( \varphi (g) p (g + t) \) \( \text{pent} (g + T) N (g) \) | 511.9 | 0 | 27 | 395 (±171) | 86 (±27) | 14.7/6.3 | 30/8 |
| | \( \varphi (g) p (g + t) \) \( \text{pent} (g + T^2) N (g) \) | 513.1 | 1.2 | 28 | 373 (±159) | 75 (±23) | | |
| *Z. polyxena*, 2011 | \( \varphi (g) p (g + t) \) \( \text{pent} (g T^2) N (g) \) | 814.8 | 0 | 35 | 337 (±79) | 252 (±64) | 10.3/3.6 | 19/9 |
| | \( \varphi (g) p (g + t) \) \( \text{pent} (g T^2) N (g) \) | 818.0 | 3.3 | 37 | 235 (±48) | 239 (±58) | | |

Notes: Model parameters: \( \varphi \), residence; \( p \), catchability; \( \text{pen} \), proportion of entering. Parameter responses: (.), not depending on sex or time; (g), sex dependent; \( t \), responding to time in a factorial manner; \( T \), responding to time in a linear manner; \( T^2 \), responding to time in a domed polynomial manner.
whereas proportional recruitments pent followed either domed patterns, with additive or multiplicative effects of sex due to the earlier appearance of males (*A. apollinus*, *Z. polyxena*); or linear decrease of males with progression of season (*Z. cerisy* in both years). Plotting the estimated daily numbers showed a short flight season with prominent peak for *A. apollinus*, 2010, and almost a month delayed and shallower peak for *A. apollinus* in 2011. *Zerynthia cerisy* flew later than *A. apollinus* in 2010, when the marking covered only a late tail of its flight. For *Z. polyxena* and *Z. cerisy* in 2011, the adult flight periods overlapped with each other and with *A. apollinus* (Figure 3). Both *Z. cerisy* and *Z. polyxena* were also still on wings, although in small

![Figure 3](image)

**Figure 3.** Estimates of the adult daily population sizes based on mark–recapture data: year 2010, when only data for *Archon apollinus* (most of flight period) and *Zerynthia cerisy* (late tail of flight period) allowed the estimation; year 2011, *A. apollinus*, *Z. cerisy*, *Zerynthia polyxena*. The error lines present standard errors of estimates, see Table 3 for model parameters.
numbers, at the end of the first May decade, whereas *A. apollinus* flight terminated at the beginning of May. The estimated population sizes were highest for *A. apollinus* (≈1000 individuals of each sex) in both 2010 and 2011, followed by *Z. polyxena* (≈300 individuals), 2011, and *Z. cerisy* (≈300 males and 100 females, i.e. a male bias), 2011.

The mean and median flight distances were shortest in *A. apollinus*, longer in *Z. polyxena* and longest in *Z. cerisy*. Males of *A. apollinus* appeared to be less mobile than females, whereas the opposite applied to *Z. polyxena* (Table 4). All three species crossed maximum distances of several kilometres, with distances > 5 km crossed by *A. apollinus* and *Z. cerisy* males.

Fitting the inverse power functions provided significant regressions for all species*sex combinations (Table 4). The fitted lines displayed significant differences (slopes: $F = 5.36, p < 0.05$, elevations: $F = 6.08, p < 0.05$; df = 9, 188). Based on the regression slopes, *A. apollinus* males moved less readily than *A. apollinus* females ($p < 0.01$), *Z. polyxena* males and females (both $p < 0.05$), and *Z. cerisy* males ($p < 0.001$) and females ($p < 0.01$). *Archon apollinus* females moved less than both sexes of *Z. cerisy* ($P < 0.05$). Disregarding sexes, *A. apollinus* dispersed less than *Z. cerisy* ($p < 0.001$) and *Z. polyxena* ($p < 0.001$), and *Z. polyxena* less than *Z. cerisy* ($p < 0.05$). Regardless of these differences, the movement probability × population size products suggested that for each species and sex, at least 10 individuals would cross a 10-km distance.

**Egg distributions on host plants**

We found 111 egg batches of *A. apollinus* [total 457 eggs, the mean/median batch egg number: 4/2 (± 4.0 SD), maximum 35 eggs], most of them on *Aristolochia rotunda* (73 batches), followed by *Aristolochia hirta* (19), *Aristolochia pallida* (18) and *Aristolochia clematitis* (1). For *Z. cerisy*, we found 31 batches [74 eggs, mean/median: 2/2 (± 1.6 SD), maximum 6] situated on *Aristolochia clematitis* (18), *Aristolochia hirta* (10) and *Aristolochia rotunda* (3). The 70 egg batches of *Z. polyxena* [total 191 eggs, mean/median: 3/2 (± 2.6 SD), maximum 11] were found in *Aristolochia rotunda* (32), *Aristolochia pallida* (30), *Aristolochia hirta* (5) and *Aristolochia clematitis* (3). We also detected cases of several species batches at the same plant: *A. apollinus* + *Z. polyxena* (60 batches), *A. apollinus* + *Z. cerisy* (6), *Z. polyxena* + *Z. cerisy* (4). These cases were ignored from the analyses below, but recalculation not ignoring them did not substantially change the results. We also ignored batches found on grass near *Aristolochia* plants (A. apollinus: 14, Z. polyxena: 1). The *A. apollinus* egg batch containing 35 eggs was also ignored, as an outlier.

Placement of *A. apollinus* egg batches (Table 5) depended on plant species (*Aristolochia rotunda* and *Aristolochia hirta* preferred, *Aristolochia pallida* intermediate, *Aristolochia clematitis* avoided). Eggs were most frequent at unfolded plants, less so on folded and never at fruiting ones. The significant interaction plant species–phenology revealed that *Aristolochia pallida* and *Aristolochia rotunda* were used during later phenological stages. Prominent plants growing in short vegetation were preferred over those growing in scrub mantles. Plants were more likely to be used if surrounded by lower cover of grasses (1-m diameter medians: 10% versus 20%, 5-m diameter: 25% versus 30%), higher cover of forbs (1-m diameter medians: 20% versus 15%), lower cover of scrubs (both medians 30%) and higher canopy closure (medians 65% versus 40%). The plants used were surrounded by more *Aristolochia* plants; this
Table 4. Basic dispersal statistics and results of fitting the inverse power functions, based on all butterfly individuals recaptured at least once.

| Butterfly species | Sex    | Mean distance ± SE | Median distance | Max. single move | Max. total distance | Equation $ln(p) = lna(±SE) - n(±SE)lnD$ | df  | $F$, $p$ | $R_{adj}^2$, $p_{10\, km}$ | $Ind_{10\, km}$ |
|-------------------|--------|---------------------|-----------------|------------------|---------------------|------------------------------------------|-----|---------|-----------------------------|-----------------|
| **Archon apollinus** | M      | 490 ± 38            | 190             | 2790             | 7610                | $ln(p) = -0.82 (±0.086) lnD -2.50 (±0.121)$ | 1,41| 89.81*** | 0.68                        | 0.017           |
|                   | F      | 550 ± 93            | 270             | 3080             | 4510                | $ln(p) = -0.51 (±0.084) lnD -2.01 (±0.132)$ | 1,17| 35.81*** | 0.66                        | 0.048           |
|                   | Both   | 490 ± 36            | 190             | –                | –                   | $ln(p) = -0.83 (±0.089) lnD -2.47 (±0.123)$ | 1,43| 88.34*** | 0.66                        | 0.020           |
| **Zerynthia polyxena** | M      | 630 ± 97            | 460             | 1920             | 4330                | $ln(p) = -0.43 (±0.134) lnD -1.79 (±0.212)$ | 1,17| 10.23**  | 0.40                        | 0.062           |
|                   | F      | 490 ± 165           | 300             | 1830             | 3690                | $ln(p) = -0.39 (±0.084) lnD -1.79 (±0.177)$ | 1,7 | 21.42**  | 0.72                        | 0.068           |
|                   | Both   | 600 ± 83            | 440             | –                | –                   | $ln(p) = -0.51 (±0.116) lnD -1.91 (±0.178)$ | 1,15| 19.41*** | 0.51                        | 0.046           |
| **Zerynthia cerisy** | M      | 830 ± 164           | 400             | 3110             | 5570                | $ln(p) = -0.38 (±0.067) lnD -1.63 (±0.110)$ | 1,15| 32.21*** | 0.66                        | 0.082           |
|                   | F      | 720 ± 180           | 640             | 1690             | 1880                | $ln(p) = -0.32 (±0.107) lnD -1.32 (±0.207)$ | 1,8 | 8.79**   | 0.46                        | 0.127           |
|                   | Both   | 810 ± 130           | 490             | –                | –                   | $ln(p) = -0.39 (±0.077) lnD -2.30 (±0.139)$ | 1,12| 25.24*** | 0.78                        | 0.041           |

Notes: All distances are in metres. $p_{10\, km}$ and $Ind_{10\, km}$ are inverse power functions-derived probability of crossing 10 km distance, and the number of individuals predicted to cross 10 km distance, based on the estimated population sizes reported in Table 3.
Table 5. Results of general linear models-regressions relating eggs records to predictors related to host plants and habitats.

| Model | Archon apollinus | Zerynthia cerisy | Zerynthia polyxena | ~ butterfly species*predictor |
|-------|------------------|------------------|-------------------|-----------------------------|
|       | df   | AIC   | Δ Dev. | df   | AIC   | Δ Dev. | df   | AIC   | Δ Dev. |
| Null (egg number~1) | 896 | 669.61 |  | 896 | 271.55 |  | 896 | 493.47 |  |
| ~ butterfly species [A] | - | - | - | - | - | - | - | - | - |
| ~ egg placement [B] | - | - | - | - | - | - | - | - | - |
| ~ a1 m [C] | 895 | 621.91 | 7.44 | 895 | 266.45 | 2.63 | 895 | 471.93 | 4.79 |
| ~ habitat [D] | 893 | 663.24 | 1.85 | 893 | 272.55 | 1.85 | 893 | 478.57 | 4.25 |
| ~ laid plants [E] | 895 | 441.06 | 34.53 | 895 | 272.98 | 0.21 | 895 | 495.43 | 0.01 |
| ~ unlaid plants [F] | 895 | 581.6 | 13.48 | 895 | 273.54 | 0.00 | 895 | 495.33 | 0.03 |
| ~ phenology [G] | 893 | 594.77 | 12.11 | 895 | 271.28 | 0.84 | 895 | 494.95 | 0.10 |
| ~ sun exposure [H] | 894 | 638.23 | 5.30 | 895 | 271.73 | 0.68 | 895 | 488.13 | 1.49 |
| ~ plant species [I] | 893 | 637.37 | 5.73 | 895 | 268.47 | 1.89 | 895 | 416.91 | 15.98 |
| ~ grass1 m [J] | 895 | 648.94 | 3.40 | 895 | 235.84 | 10.28 | 895 | 478.92 | 3.37 |
| ~ grass5 m [K] | 895 | 652.26 | 2.90 | 893 | 244.86 | 12.13 | 893 | 490.7 | 1.78 |
| ~ forbs1 m [L] | 895 | 666.44 | 0.77 | 894 | 260.74 | 5.49 | 894 | 496.92 | 0.11 |
| ~ forbs5 m [M] | 895 | 670.36 | 0.19 | 893 | 221.48 | 20.80 | 893 | 475.2 | 4.94 |
| ~ scrub10 m [N] | 895 | 666.24 | 0.80 | 895 | 260.45 | 4.86 | 895 | 488.49 | 1.42 |
| ~ trees10 m [O] | 895 | 640.62 | 4.64 | 895 | 238.04 | 13.17 | 895 | 490.23 | 1.07 |
| Two-way interactions | |  |  | | | | | | |
| ~ D: I | 881 | 652.27 | 1.45 | 881 | 231.03 | 6.77 | 882 | 442.48 | 11.14 |
| ~ I: G | 882 | 586.56 | 11.57 | 881 | 217.55 | 13.08 | 882 | 480.48 | 3.58 |
| Multiple-regressions | |  |  | | | | | | |
| ~ D + H + G + D + I + O + L | 882 | 292.81 | 60.63 | - | - | - | - | - | - |
| ~ I + G + H + O + C | - | - | - | 886 | 181.49 | 40.83 | - | - | - |
| ~ E + I + O + D + N + C | - | - | - | - | - | - | 886 | 364.64 | 30.28 |
| ~D + J + B + F | - | - | - | - | - | - | - | 197 | 895.8 | 24.14 |

Notes: Models for Archon apollinus, Zerynthia cerisy and Zerynthia polyxena compared plants with egg batches of the focal species against all other plants, including those with negative records. Models ~ butterfly species*predictor compared egg batch sizes among the three species, disregarding plants with negative records.
applied to surrounding plants not bearing and bearing butterfly eggs, and the latter predictor yielded the strongest fit of all single-factors models.

The preferred *Z. cerisy* host plant was *Aristolochia clematitis*, followed by *Aristolochia hirta*. Eggs were frequent at fruiting or flowering plants, never at unfolded plants. Plants growing freely or under scrubs were preferred over those in forest mantles. The preferred plants grew under low scrub (medians: 25\% versus 30\%) and canopy (medians: 10\% versus 50\%) covers.

The preferred *Z. polyxena* plant was *Aristolochia pallida*, followed by *Aristolochia rotunda*; the remaining two plants were rarely used. All four habitats were used, although closed forest and open woodland prevailed. The significant interaction of plant species–habitat revealed that *Aristolochia clematitis* was most often used in scrub. Unfolded and flowering plants were used more often than fruiting ones. Preferred plants were surrounded by higher cover of forbs (5-m diameter medians: 25\% versus 20\%), lower covers of scrubs in 10 m (both 1-m and 5-m diameter medians: 30\%) and lower canopy closure (medians: 30\% versus 45\%).

All three forward-selected models contained plant species and canopy closure (trees10); laid plants and biotope entered models for *A. apollinus* and *Z. polyxena*; plant placement and phenology for *A. apollinus* and *Z. cerisy*; and amount of adjoining host plants (a1 m) for *Z. cerisy* and *Z. polyxena*.

Mutual comparison among the three butterflies revealed that *A. apollinus* produced the largest batches and *Z. cerisy* the smallest batches. All three species preferred ventral leaf sides. The significant interaction species–habitat revealed that *Z. cerisy* was the only species ovipositing in arable fields. As for the plant species, *Z. cerisy* preferred *Aristolochia hirta* (Figure 4a). The significant interaction species–phenology showed that *Z. polyxena* used folded plants. *Zerynthia cerisy* favoured plants growing under sparser canopy (median: 10\%) than *Z. polyxena* (30\%) and *A. apollinus* (60\%) (Figure 4b).

**Larval counts**

We found 112 larval groups of *A. apollinus* [total 278 larvae, the mean/median group size: 2/2 (± 1.9 SD), maximum 10 larvae], 89 groups of *Z. polyxena* [total 196 larvae, mean/median: 2/1 (± 1.9 SD), maximum 10], and 18 groups of *Z. cerisy* [total 28 larvae, mean/median: 2/1 (± 0.7 SD), maximum 3] (Figure 4c). *Archon apollinus* larvae were most commonly found on *Aristolochia rotunda* (71), followed by *Aristolochia hirta* (26), *Aristolochia pallida* (10) and *Aristolochia clematitis* (5). *Zerynthia cerisy* larvae were found on *Aristolochia hirta* (9), *Aristolochia clematitis* (6) and *Aristolochia rotunda* (3). *Zerynthia polyxena* were recorded on *Aristolochia rotunda* (57), *Aristolochia pallida* (23), *Aristolochia clematitis* (8) and *Aristolochia hirta* (1). We also detected cases of more than one species feeding at the same plant (*A. apollinus* + *Z. polyxena*: 2, *A. apollinus* + *Z. cerisy*: 2, *Z. polyxena* + *Z. cerisy*: 1); these cases were ignored in subsequent analyses. Early instars of *A. apollinus* larvae were feeding inside flowers, including the large, subterranean flowers of *Aristolochia hirta* (n = 3) (Figure 2h). Groups of medium-sized larvae built silk-woven tents from host plant leaves (Figure 2k), staying there during the morning and evening hours and leaving the tents to feed and bask at midday. In contrast, *Z. cerisy* and *Z. polyxena* fed in exposed positions.
As with eggs, *A. apollinus* larvae were most frequent found on *Aristolochia hirta*, followed by *Aristolochia rotunda, Aristolochia pallida* and *Aristolochia clematitis* were rarely used (Table 6). Most of the larvae were in third to fifth instars during the search. Most of the plants used were already flowering or fruiting. The larval occupancy was not affected by the density of *Aristolochia* stems in 1-m diameters, but was affected by the number of leaves (occupied ≈70, unoccupied ≈40).

*Zerynthia cerisy* larvae were found most frequently at *Aristolochia clematitis* and *Aristolochia hirta*, less so at *Aristolochia rotunda*, and never at *Aristolochia pallida*. Most of the larvae were in first to second instar, most of the plants used were already flowering or fruiting. The occupied plants were surrounded by low *Aristolochia* stem density (occupied ≈5, unoccupied ≈10), and hence leaf density (occupied ≈30, unoccupied ≈45), but the significant interaction of stem—leaf density revealed that the larvae preferred isolated but richly leafed plants.

*Zerynthia polyxena* larvae distinctly preferred *Aristolochia pallida* over *Aristolochia rotunda* and *Aristolochia clematitis*, whereas *Aristolochia hirta* was least preferred. The larvae were mostly in the first to third instars. Host plant phenology, surrounding stem density and surrounding leaf number had no effects.

Mutual comparison among the three species corroborated that *Z. polyxena* larvae were more abundant on *Aristolochia pallida* and *Aristolochia rotunda*. More *Z. polyxena* larvae were found on plants with high amount of leaves consumed.
Table 6. Results of general linear models-regressions relating larval records to predictors related to host plants and habitats.

| Model | Archon apollinus | Zerynthia cerisy | Zerynthia polyxena | ~ butterfly species*predictor |
|-------|------------------|------------------|--------------------|-------------------------------|
| df    | AIC | Δ Dev. | p  | df | AIC | Δ Dev. | p  | df | AIC | Δ Dev. | p  | df | AIC | Δ Dev. | p  |
| Null (larvae number~1) | 257 | 355.17 |  | 257 | 132.57 |  | 257 | 334.44 |  | 218 | 809.97 |  |
| ~ butterfly species [A] | 256 | 354.53 | 0.75 |  | 256 | 121.83 |  | 256 | 336.44 |  | 216 | 807.12 | 2.72 * |
| ~ a1 m [B] | 256 | 333.93 | 23.239 |  | 256 | 122.91 |  | 256 | 334.98 | 0.44 | 213 | 810.49 | 1.08 |
| ~ instar [C] | 252 | 312.76 | 52.405 *** |  | 252 | 107.41 | 26.92 *** |  | 252 | 291.08 | 16.05 *** | 207 | 809.77 | 6.26 . |
| ~ leaf1 m [D] | 254 | 351.26 | 2.8 |  | 254 | 130.22 | 6.39 * |  | 254 | 337.39 | 0.92 | 207 | 914.29 | 4.42 . |
| ~ plant species [F] | 254 | 339.58 | 6.11 |  | 254 | 104.56 | 26.04 *** |  | 254 | 308.88 | 9.49 *** | 208 | 805.94 | 7.01 * |
| ~ D*B | 243 | 312.76 | 3.09 ** |  | 243 | 114.62 | 9.42 ** |  | 243 | 336.02 | 0.89 | 207 | 803.57 | 4.47 . |
| ~ F*E | 237 | 313.28 | 13.67642 *** |  | 237 | 115.12 | 8.77 |  | 237 | 115.12 | 8.77 | 188 | 825.01 | 15.54 . |
| ~ C + D + F: E | 248 | 72.44 | 59.84 *** |  | 248 | 72.44 | 59.84 *** |  | 248 | 72.44 | 59.84 *** | 188 | 825.01 | 15.54 . |
| ~ F + C + D | 249 | 256.84 | 28.16 *** |  | 249 | 256.84 | 28.16 *** |  | 249 | 256.84 | 28.16 *** | 188 | 825.01 | 15.54 . |
| ~ A + D + F + C | 213 | 793.57 | 12.87 *** |  | 213 | 793.57 | 12.87 *** |  | 213 | 793.57 | 12.87 *** | 188 | 825.01 | 15.54 . |

Notes: Models for *Archon apollinus, Zerynthia cerisy* and *Zerynthia polyxena* compared plants bearing larvae of the focal species against all other plants, including those with negative records. Models ~ butterfly species*predictor compared larval distribution among the three species, disregarding plants with negative records.
Considering instars (Figure 4d), the results were roughly the same as in models with negative records. All forward-selected models included plant species and larval instar.

**Discussion**

The phenology of the system composed of four spring-blooming *Aristolochia* plants and three spring-flying papilionid butterflies reflected yearly weather. In 2010, adults of the earliest-flying *A. apollinus* appeared during the third week of March, rapidly reached peak numbers and ceased flying in early April, whereas the two other species were barely appearing. Three weeks later, the encountered *Z. cerisy* and *Z. polyxena* were often worn individuals. Some adults of the latter two species, however, were still on wings a month later. In 2011, when the spring was unusually cold, no *A. apollinus* appeared before the first week of April, and all three species flew simultaneously.

Comparisons of sympatric species that aimed to disclose details of their resource niches are easier for species occurring simultaneously in time [e.g. space utilization by Eumaeini lycaenids: Prieto and Dahners (2009); or a study of co-occurring dragonflies: Khelifa et al. (2013)].Analyses of butterfly oviposition preferences with regard to host plant conditions may provide guidance for conservation management (e.g. Jansen et al. 2012; Šlancarová et al. 2012). Due to sequential phenology, however, the system described in this paper does not present an ideal time for studying immature distribution – any recording date would be too early or too late for some butterfly–plant interactions. Our findings on egg and larval preferences therefore describe only snapshots of the whole system dynamics, overcoming this limitation would require following pre-tagged plants, and associated butterfly immature, for the entire spring (cf. Table 1).

**Adult biotope use**

In the highly heterogeneous submediterranean biotope mosaic, all studied species were encountered in all available habitats, but there were clear differences: the phenologically postponed *Z. cerisy* preferred open woodland over scrub, contrasting with the earlier-appearing *A. apollinus* and *Z. polyxena*; and females of all three species were more frequently than males encountered in close forest, which they probably entered for oviposition. Using adjacent components of vegetation mosaic for different activities is common in butterflies. Slamova et al. (2013) observed that adults of *Erebia aethiops* visited sites with shady microclimates during the hottest time of day, and Bergman (2001) observed that females of *Lopinga achine* spent much time within forest gaps containing host plants, whereas males stayed in dense understory. Dennis et al. (2003) warned against viewing insect habitats as equivalents to phytosociological units with homogeneous vegetation, because a species may locate different resources in different vegetation types.

**Adult demography and dispersal**

For 2 years, *A. apollinus* was consistently the most abundant of the three study species, followed by *Z. polyxena* and *Z. cerisy*.

Residency values (and hence, daily and average survival), obtained from mark–recapture data, did not deviate from those reported for other univoltine spring-flying
butterflies (e.g. Vlasanek et al. 2009; Celik 2012). In cases when sexes differed, males displayed higher residency than females, contrasting with the distantly related spring-flying papilionid *Parnassius mnemosyne* (Vlasanek et al. 2009) or with a population of *Z. polyxena* in Slovenia (Celik 2012). Lower female residency indicates either increased mortality or increased emigration. As we detected higher female mobility in all three species, emigration provides a plausible explanation.

*Archon apollinus* was the most sedentary species, followed by *Z. polyxena* and *Z. cerisy*. Abundances (and hence local densities) followed the reverse pattern, pointing to a density–mobility trade off. Inverse mobility–density relationships were detected, e.g. for British (Cowley et al. 2001) and Central European (Bartonova et al. 2014) butterfly faunas, and observed empirically by Konvicka et al. (2012) for butterflies co-occurring in humid grasslands. Butterflies using widespread but sparsely distributed resources employ higher mobility to compensate for low resource density.

The low *A. apollinus* mobility agrees with Hesselbarth et al. (1995), who nevertheless expected females to be more sedentary than males, contrary to our finding. The low mobility might be linked to the short time available for dispersal in early spring (cf. Vlasanek et al. 2009). For *Z. polyxena*, the mobility reported here is higher than that observed in Slovenia (Celik 2012), or in the closely related Italian species *Zerynthia cassandra* Geyer, 1828 (Vovlas et al. 2014). Detecting long-distance movements using mark–recapture depends on the study area size (cf. Zimmermann et al. 2011), which might explain these discrepancies. Still, *Z. polyxena* is generally viewed as a sedentary species in more northerly parts of Europe (Weidemann 1995; Dapporto 2010), possibly because of regional differences in resources supply and distribution. Whereas four host plants with varying phenology are used in Greek Thrace, a single host (*Aristolochia lutea*) was used by the Slovenian population (Celik 2012), and another single host (*Aristolochia clematitis*) is used in Central Europe (Benes et al. 2002). With several potential larval hosts growing in various habitats, ovipositing females may benefit from wider landscape exploration, whereas in single-host situations, females should be faithful to host plant patches. Finally, the high *Z. cerisy* mobility may reflect its flight in later spring, when the weather becomes more favourable, but locating sun-exposed host plants becomes increasingly difficult.

**Requirements of pre-adult stages**

Each of the three butterflies oviposited and fed on several phenotypically different *Aristolochia* species, suggesting that chemical clues, rather than larval morphology, are used to locate oviposition substrates (e.g. Mebs and Schneider 2002). The four *Aristolochia* plants consumed varied in phenology (*Aristolochia pallida* was the earliest sprouting, *Aristolochia clematitis* the latest sprouting) and biotope association (*Aristolochia hirta* prevailed in closed forest, *Aristolochia pallida* in open forest, *Aristolochia rotunda* in scrub, *Aristolochia clematitis* on disturbed grounds), and their use by the butterflies reflected these patterns.

*Archon apollinus* and *Z. polyxena* used all four *Aristolochia* species, corroborating reports on their wide host ranges (cf. Tolman and Lewington 2009) and refuting the claims that *Aristolochia clematitis* is toxic for *A. apollinus* (Carbonell 1991; Köstler 1993). Immatures of the late-flying *Z. cerisy* did not use *Aristolochia pallida*, which was mostly senescent during its flight. Immatures of *A. apollinus* were relatively frequent in closed forest, arguably because its adults oviposit before the leaf flush,
similarly to other early-spring woodland butterflies [e.g. *Anthocharis cardamines* (Linnaeus 1758): Dempster (1997); or *Hamearis lucina* (Linnaeus 1758): Sparks et al. 1994]. On the other hand, some immatures of the late-flying *Z. cerisy* were located on *Aristolochia* plants growing in recently abandoned fields, or on stream gravel beds. These sites do not get shaded later in the season and using disturbed habitats is often linked to increased mobility (Dennis et al. 2004), which was the case here.

All three butterflies preferred sites with high *Aristolochia* shoot densities, similarly to the Cretan endemic *Zerynthia cretica* (Dennis 1996). Plants growing in higher densities, or just larger plants, are better detected by females, provide more food for the larvae, and offer better cover from parasitoids or predators (Renwick and Chew 1994). *Archon apollinus* and *Z. polyxena* eggs were frequent at plants with other egg-bearing plants in their vicinity. Such accumulations of eggs may result from visits to an identical spot by several females (Hesselbarth et al. 1995), or from recurrent visits of a female to the same plant (Tolman and Lewington 2009). Restricted time available for flight in early spring might be responsible for recurrent visits. Another trait shared by *A. apollinus* and *Z. polyxena* was their preference for host plants surrounded by forbs, rather than grasses. As both species oviposit on young plants, the surrounding vegetation probably serves as clue for future host plant size. For *Z. cerisy*, both Tolman and Lewington (2009) and Hesselbarth et al. (1995) describe oviposition at shady spots, in contrast to our records. It is possible that their descriptions reflected conditions in warmer parts of the *Z. cerisy* range, where the females might prefer cooler spots than at our locality, situated near the northern border of the species’ range.

The use of several host plant species that appear sequentially in different habitats clearly enhances the regional resource base for the butterflies, arguably buffering their population dynamics against risks of phenological mismatches with their plants (Cushman et al. 1994; Van Asch and Visser 2007). This highlights the importance of a finely structured habitat mosaic, where alternative host plants grow in relatively close proximity, within reach of dispersing butterflies (cf. Dennis et al. 2003).

Different situations, however, exist elsewhere in Europe. Jordano and Gomariz (1994) reported from Spain that because potential host plants of *Zerynthia rumina* (Linnaeus 1758) are rarely sympatric, host plant use by the butterfly varies among its populations. *Zerynthia cretica* is reportedly monophagous on the Cretan endemic *Aristolochia cretica*, although other congeneric plants occur on the island (Dennis 1996). A single host plant is also used by the *Z. cassandra* population studied by Vovlas et al. (2014) in Italy, the Slovenian *Z. polyxena* studied by Celik (2012), and all *Z. polyxena* populations in Central Europe (Batary et al. 2008).

**Conclusion**

As the three *Aristolochia*-feeding papilionids follow a phenological sequence in adult and larval emergence and use overlapping ranges of host plants, which themselves differ in phenological patterns and prevail in different successional stages of Mediterranean vegetation, the co-occurrence of the butterflies appears to be facilitated by their ability to locate resources in different, but closely adjacent, environments (cf. Oliver et al. 2010). Considering the local population sizes and dispersal ability of the three studied butterflies relative to the patchiness of landscape mosaic in
the area studied, none of them seems to be currently threatened by host plant or habitat loss. This certainly applies for the EU-protected *Zerynthia polyxena*, a species that is still widespread in Greece (Pamperis 1997). Still, the heterogeneous patchworks of open, semi-open and closed vegetation, typical for ancient cultural landscapes of the Mediterranean, may be lost to spontaneous forest encroachment if left unmanaged, or even actively planted by trees. The crucial role of landscape heterogeneity for invertebrates is increasingly recognized from human-altered areas of northern Europe (e.g., Samways 2007; Shreeve and Dennis 2011; Slancarova et al. 2014) and might be even more prominent in the Mediterranean, a region hosting many more species and currently experiencing rapid land use changes (Atauri and De Lucio 2001; Kati et al. 2012; Fernández-Chacón et al. 2014).

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