

Climate change versus ecological drift: Assessing 13 years of turnover in a butterfly community

Vasiliki Sgardeli*, Konstantina Zografou, John M. Halley

*Department of Biological Applications and Technology, University of Ioannina,
Metavatiko Building, Ioannina 45110 Greece*

Received 18 March 2015; accepted 31 December 2015
Available online 6 January 2016



Abstract

Various studies document the ecological impacts of climate change on many species and environments, ecosystem processes and species interactions (e.g. the timing of host-plant flowering and butterflies' phenology). However, what is usually overlooked is that populations drift even in the absence of environmental stress. Ecological drift can lead to changes in community composition that can easily be mistaken for an environmental trend. We demonstrate how the neutral model of biodiversity can be used to simulate ecological drift and thus assess the significance of observed changes. We apply this method to the butterfly community of Dadia National Park, Greece, for which there is indication of a community shift due to temperature rise. We found that the observed turnover in the sampled habitats is greater than the expected neutral turnover. This has a probability of less than 2.5% to have occurred by chance (Wilcoxon signed-rank test). We also found a significant increase of the population of warm-adapted species, confirming the results of an earlier study of the same community. Nevertheless, neutral turnover still explains much of the observed variability. We argue that null models are essential to the interpretation and attribution of observed changes in species composition in the presence of regional or global environmental change.

Zusammenfassung

Viele Untersuchungen dokumentieren die ökologischen Auswirkungen des Klimawandels auf verschiedene Arten, Lebensräume, Ökosystemprozesse und interspezifische Interaktionen. Indessen wird häufig übersehen, dass Populationen sich auch verändern, wenn starke Stressoren fehlen. Zufällige ökologische Drift kann zu Veränderungen in der Gemeinschaftszusammensetzung führen, die leicht mit einem umweltbedingten Trend verwechselt werden können. Wir zeigen, wie das neutrale Modell der Biodiversität genutzt werden kann, um ökologische Drift zu simulieren und damit die Signifikanz von beobachteten Änderungen zu bestimmen. Wir wenden diese Methode auf die Schmetterlingsgemeinschaft des Dadia-Nationalparks (Griechenland) an, bei der es Hinweise auf eine durch Temperaturerhöhung verursachte Änderung der Gemeinschaft gab. Wir fanden, dass der beobachtete Turnover in den untersuchten Habitaten größer war als der erwartete "neutrale" Turnover. Die Irrtumswahrscheinlichkeit hierfür ist geringer als 2.5% (Wilcoxon-Vorzeichen-Test). Wir fanden ebenfalls eine signifikante Zunahme

*Corresponding author. Tel.: +0030 6945013513.
E-mail address: wiki.sgardel@yahoo.gr (V. Sgardeli).

von warm-adaptierten Arten. Dennoch erklärt der neutrale Turnover einen hohen Anteil der beobachteten Variabilität. Wir sind der Auffassung, dass Nullmodelle unverzichtbar sind für die Interpretation und Zuschreibung von beobachteten Änderungen der Artenzusammensetzung bei regional oder global auftretenden Umweltveränderungen.
© 2016 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

Keywords: Neutral model; Null model; Ecological drift; Climate change; Dada National Park

Introduction

The detection of the effects of long-term forces on ecological communities is a major challenge for ecologists today. Many studies document the northward (or altitudinal) shift or expansion of species ranges (Holbrook, Russell, & Stephens 1997; Sagarin, Barry, Gilman, & Baxter 1999; Meshinev, Apostolova, & Koleva 2000; Walther et al. 2002; Poloczanska et al. 2013). To make the connection with climate change, a common approach is to show that the observed changes in a community over time are consistent with the expected changes under a projected scenario. Given the possible bias toward publishing of studies that confirm the effects of climate change, it is important to keep in mind the statistical significance of the results. The main complication is that ecological communities are constantly changing due to demographic stochasticity (ecological drift), even when environmental and other conditions are static (Vellend 2010). Hence, before accepting any alternative hypothesis one must show that the observed changes cannot be explained by ecological drift alone (null hypothesis). This is analogous to the attribution problem of global warming itself (Halley & Kugiumtzis 2011). The aim of this article is to: (a) emphasize the important role of ecological drift in the evolution of ecological communities, (b) demonstrate how the neutral model can be used as a null model to simulate ecological drift and test the null hypothesis and (c) apply this to a community of butterflies for which there is indication of climate-induced changes in community composition.

The neutral theory of biodiversity was introduced in ecology by Hubbell (2001) with the aim of explaining community composition as the result of demographic stochasticity and dispersal. The model produces realistic ecological patterns based on a minimum set of assumptions, including equal reproductive and dispersal ability for all species. This has proven a very successful approximation to reality and a valuable null model (Hubbell 2001; Chave, Muller-Landau, & Levin 2002; Volkov, Banavar, Hubbell, & Maritan 2003; Halley & Iwasa 2011; Rosindell, Hubbell, He, Luke, & Etienne 2012). Although there are other models of community drift, the neutral model pioneers in one important aspect: apart from demographic stochasticity, it takes into account the stochasticity due to dispersal limitation. Because of dispersal limitation, the composition of local samples differs from that of the regional community, thus the model incorporates the sampling effects that arise when local samples

are drawn from a community (see Etienne and Alonso 2007). The neutral model has been used to assess species temporal turnover in real communities (e.g. Leigh, Wright, Herre, & Putz 1993; McGill, Hadly, & Maurer 2005; Gilbert, Laurance, Leigh, & Nascimento 2006; Dornelas et al. 2014). Such methods assume that the real community drift at equilibrium is well approximated by neutral drift. Thus, any deviation from the model predictions is attributed to external forces causing systematic drift.

Butterflies are an excellent group for examining the effects of global change on populations. They react faster than other groups (Devictor et al. 2012) and due to their short life cycle, changes in their distribution, abundances and community composition can be visible over a short time period (Robinson, Armstead, & Bowers 2012). The best documented effect on butterfly populations as climate warms is geographic range expansions to cooler areas, toward higher latitudes or altitudes (Parmesan and Yohe 2003). There is evidence that the rate at which species are invading from low altitudes or latitudes is faster than the rate at which the inhabitant species are receding poleward (Sagarin et al. 1999; Walther et al. 2002). As a result, species related to warm conditions begin to invade ecological communities (Barry, Baxter, Sagarin, & Gilman 1995; Wilson, Gutiérrez, Gutiérrez, & Monserrat 2007; Dapporto and Dennis 2013). Yet, there is a considerable asymmetry in the degree and direction of these changes among different groups and localities (Devictor et al. 2012).

Here, we use the neutral model to assess the observed changes in a butterfly community in a period of 13 years. We compare the turnover of the real communities with the turnover expected by neutral drift. If the observed turnover is significant (i.e. not explained by neutral drift), the temperature-rise effect is plausible and can be further assessed. If, on the contrary, the model explains the observed turnover, the temperature-rise effect hypothesis is not valid. We compare our results with those of Zografou et al. (2014), where statistical methods were used to reveal significant changes in the same butterfly community. Note that our approach is fundamentally different from that of Zografou et al. (2014). While statistical tests can reveal significant changes in community composition on the basis of observed or assumed distributions, they do not take into account community dynamics. This means that a change termed significant by a statistical test might be an expected change under ecological drift (and the opposite). Based on the above, we expect our approach to refine and complement the results of

Zografou et al. (2014) by revealing as “significant” only the changes that are not explained by ecological drift.

Materials and methods

Data

Our study area is the Dadia–Leukimi–Soufli National Park (Dadia NP), Greece, previously studied by Zografou et al. (2014). Dadia NP is located in northeastern Greece and is part of the NATURA 2000 network. The reserve has remained relatively unmodified by human influence for the last 30 years. As reported by Zografou et al. (2014), there was a significant temperature rise in the area between 1990 and 2012, which was consistent with the observed changes in species composition (increased alpha diversity of warm-adapted species). We use butterfly abundance data collected in 1998 and 2011. The 1998 data were collected by Grill and Cleary (2003) and the same areas were re-sampled by Zografou et al. (2014) following the same sampling scheme. The data come from seven sampling areas, each corresponding to a different habitat type: Agriculture (AG), Dry Meadow (DM), Grazed Pasture (GP), Mixed Forest (MF), Oak Forest (OF), Pine Forest (PF) and Wet Meadow (WM). The size of the samples (12 km²) is small compared to Dadia NP area (432 km²), which allows us to consider them as local samples.

Model

We use the implicit-space neutral model of biodiversity to approximate the drift of the real samples. Each local sample is treated as a local community in Hubbell’s sense, where individuals of all species compete for a fixed number of sites associated with resources (zero-sum game). Furthermore, all individuals regardless of species have the same birth and death rates, where the birth rate is related to the probability that the offspring of a given individual will colonize an empty site; that is to say individuals have the same reproductive success. Each local community is connected to a regional community (metacommunity) through immigration. In particular, for every death event in the local community, there is a fixed probability that a random individual from the metacommunity will colonize the site that is left unoccupied by the death.

To parameterize the model we follow usual methodology, estimating the parameters that maximize the likelihood of the observed data (Etienne 2005; Jabot, Etienne, & Chave 2008). However, we introduce a different parameterization of the regional community, by determining its size independently, based on estimates of regional diversity that exist for our study area. We assume that: (a) the seven sampled areas are independent local samples from the same metacommunity and (b) the metacommunity has a fixed rank-abundance distribution of the log-series form. Fixing the distribution is

justified by the fact that the metacommunity turnover times are much larger than those of the local communities, hence the metacommunity distribution does not change significantly during the time scale of examination. The log-series distribution is used since it is a good approximation of the zero-sum-multinomial but easier to handle.

The second step is to determine the size of the metacommunity, J_m , the fundamental biodiversity parameter, θ , (Hubbell 2001) and the immigration probabilities for each local sample m_j . Since there is a lack of data to estimate the metacommunity parameters independently, we use a combination of reported values and maximum likelihood estimates from available data. We set the number of species in the metacommunity equal to the reported number of butterfly species in Evros (regional unit of Greece containing Dadia NP), $S_m = 128$ (Pamperis 2009). We then find $\theta = 13.5$ by maximizing the likelihood of the observed pooled sample rank-abundance distribution. Using the log-series species-individual curve, we estimate the metacommunity size to $J_m = 172,260$ individuals. Finally, the immigration probabilities for each local sample are estimated using Etienne’s sampling formula (Etienne 2005) as applied by Jabot et al. (2008). However, instead of using the pooled sample as the metacommunity species-abundance vector, as proposed by Jabot et al. (2008), we use the log-series metacommunity defined above. The estimated parameters and methods of estimation are analytically presented in Appendix A.

Simulations

For each of the seven observed samples we produced a set of simulated neutral samples by performing direct simulations of the neutral stochastic process (see Appendix C). The produced samples correspond to possible states of the local communities when these are at dynamical equilibrium. To produce one sample we let the simulation run until the process reached stationarity (dynamical equilibrium) and recorded the species-abundance vector at the end of the simulation. The time needed to reach the stationary state is empirically found to be approximately 10,000 generations. In simulation terms, one generation is defined as the time interval required for all existing individuals in the community to be replaced. Although some butterfly species can have more than one generation within the growing season we chose to model the population yearly, namely the adult population of each year is replaced by the adult population of the next year, ignoring any intermediate replacements. This way, one generation time in the simulation corresponds to one year’s time. The Fortran95 code developed to perform the simulations is provided in Appendix C.

Temporal turnover estimation

Temporal turnover refers to the change of a community’s composition in time. Here we measure the change of the

species-abundance vector of each local sample in 13 years. As a measure of turnover we use the Bray–Curtis dissimilarity index between an abundance vector sampled at time t and the same vector sampled at time $t + \Delta t$:

$$BC = \frac{\sum_{i=1}^S |n_{t,i} - n_{t+\Delta t,i}|}{\sum_{i=1}^S n_{t,i} + n_{t+\Delta t,i}}, \quad (1)$$

with $n_{t,i}$ and $n_{t+\Delta t,i}$ the abundances of species i at the two instances, S the total number of species found in both samples (the union) and $\Delta t = 13$ years. Because the samples taken from the same habitat in 1998 and 2011 differ in size, before applying Eq. (1) we re-sampled the bigger sample (either 1998 or 2011) and re-estimated the dispersal probabilities (m_j) (see Appendix A).

To estimate the turnover of the corresponding neutral samples we performed simulations using the 1998 parameterization. For each sample we performed the simulation for 13 years at stationarity, recording the species-abundance vector at the beginning and the end of the simulation. We repeated 1000 times to get 1000 sets of vectors 13 years apart and applied Eq. (1). To estimate the change in abundance of separate species we simulated 10,000 years of stationarity and kept record of the abundances of all species each year. We then selected an initial abundance value N_0 (from 0 to 150); identified all species that had this abundance at some point in time and their abundances after 13 years. This way we constructed the distribution of abundances after 13 years, for each initial abundance, N_0 .

Results

The 1998 and 2011 samplings recorded 2884 and 3248 individuals representing 70 and 78 species, respectively. In both years a total of 88 species were recorded, with the most abundant species being *Aporia crataegi* in 1998 and *Aricia agestis* in 2011 (see Zografou et al. 2014 for more information). The results of the maximum likelihood parameter estimation are summarized in Appendix A: Tables 1 and 2. To assess the parameterization we compared the rank-abundance distributions of the observed and the simulated samples (see Appendix B: Figs. 1 and 2). For all samples, the observed distributions fall within the range of the 1000 neutral distributions, hence the parameterization is good. By pooling the data of each year we obtained the pooled sample rank-abundance distribution, which is compared with 1000 random samples from the neutral metacommunity. The agreement between the observed pooled sample and the metacommunity samples is not as good (see Appendix B: Figs. 1 and 2). This means that the pooled sample cannot be considered a random sample from the metacommunity.

In Fig. 1 we compare the turnover of the real samples with the turnover distribution of the simulated samples. The turnover in the three forest habitats and the Grazed Pasture habitat is significantly greater than that expected by the model

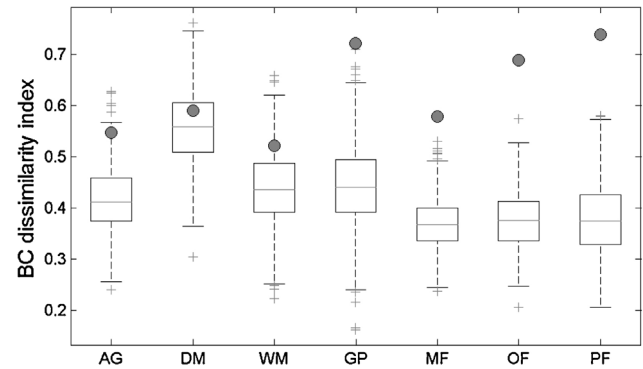


Fig. 1. Observed temporal turnover between 1998 and 2011, measured as the Bray–Curtis dissimilarity index (gray circles) and the corresponding neutral turnover of 1000 neutral communities (boxes) for each of the seven habitat types (local samples) (AG = Agriculture, DM = Dry meadow, WM = Wet meadow, GP = Grazed pasture, MF = Mixed forest, OF = Oak forest, PF = Pine forest). Boxes define the upper and lower quartiles of the distribution of neutral turnover, whiskers extend to 1.5 times the interquartile range and horizontal lines represent the median. The real turnover is computed after re-sampling the bigger sample (either 1998 or 2011) (see Appendix A: Table 2). The observed turnover is significantly greater than the neutral turnover for the three forest habitats (MF, OF, PF) and the GP habitat.

($p < 0.004$), while in the rest of the habitats it lies within 95% of the neutral distributions. In all habitats the observed turnover is greater than the average neutral turnover, which has less than 2.5% probability to be due to chance (Wilcoxon signed-rank test).

To see how particular species affected the turnover, we plotted the abundance of every species in 2011 against its abundance in 1998 along with the 95% confidence intervals of the distribution of simulated abundances (Fig. 2). In most habitat types (except Agriculture and Wet Meadow) there are species abundances that lie outside the 95% confidence intervals. We identified 16 such cases, which correspond to 11 species (out of the 88 species studied). Almost all of these species increased their abundance except for *A. crataegi* and *Argynnis paphia*. Furthermore, three species (*A. agestis*, *A. crataegi* and *Kirinia roxelana*) showed significant increase or decrease in more than one habitat. These species are listed in Table 1, along with the 19 species that were reported by Zografou et al. (2014) to contribute the most to turnover. From those 19 species, only seven had an observed trend in abundance that cannot be attributed to drift. Furthermore, we found four other species whose change in abundance is greater than expected by drift. Table 1 also reports the Species Temperature Index (STI); that is the mean temperature value per species across its range (data taken from Schweiger, Harpke, Wiemers, & Settele 2014). In conjunction with the STI values, our results show that species with high STI (warm-adapted) increased their abundance, while species with low STI (cold-adapted) either increased or reduced their abundance.

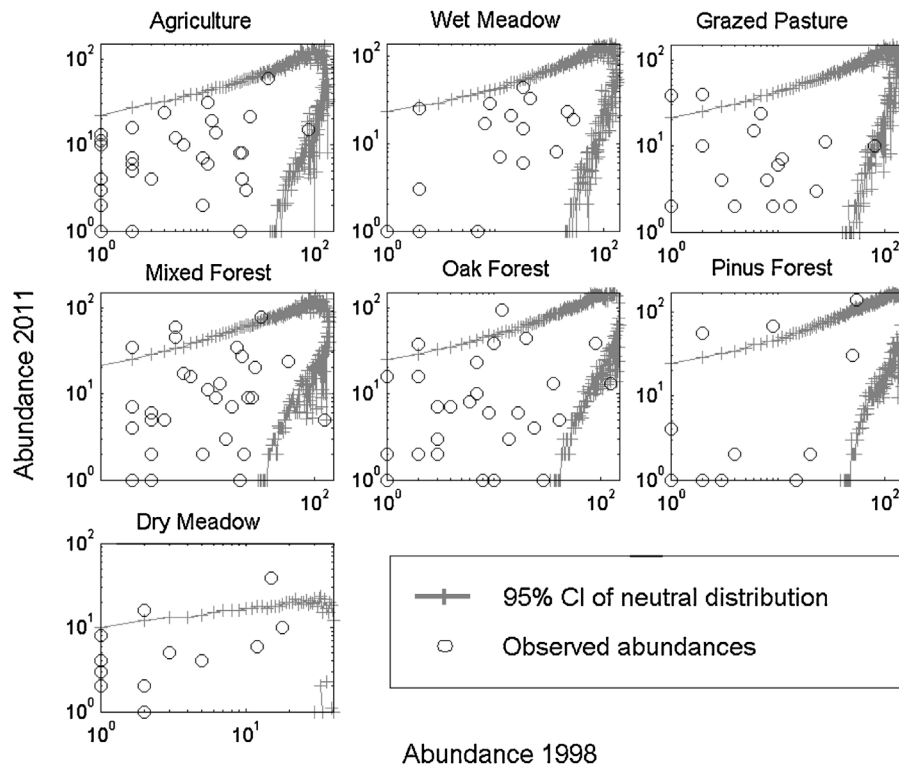


Fig. 2. Observed species abundances in 2011 versus their abundances in 1998 (open circles) and 95% confidence intervals (CI) of the corresponding distribution of simulated neutral abundances (gray lines). Simulated data are drawn from stationarity by picking random species with a given abundance and finding the distribution of abundances after 13 years. The real data are plotted after re-sampling the bigger sample (either 1998 or 2011) to make the 1998 and 2011 samples comparable in size (see Appendix A: Table 2).

Discussion

A large number of papers reported changes in ecological communities and attributed them to climate change. However, that these observed trends might simply be due to ecological drift is not usually tested. In this paper we used the implicit-space neutral model of biodiversity to assess the observed temporal turnover in a butterfly community that had been studied earlier using statistical methods (Zografou et al. 2014). Although statistical tests can reveal significant changes in community composition, they cannot exclude the possibility that these changes are due to ecological drift. Our approach, which estimates natural community drift, refines the null hypothesis: natural (non-climatic) processes can produce the observed turnover. Indeed, we found that neutral drift explains most of the observed variation in abundance; still there is a considerable number of species whose change in abundance is not explained by drift and a significant community turnover in four out of seven habitats studied. Thus, the null hypothesis is rejected.

The drift model revealed a significant increase in abundance of warm-adapted species (i.e. species with high Species Temperature Index), consistent with the temperature rise recorded in Dadia NP since 1990 (Zografou et al. 2014). The above is in agreement with the study of Zografou et al. (2014), which reported an increased alpha-diversity of warm-adapted

species and an increase of the Community Temperature Index. At the level of species, we found that the observed trends of 11 species could not be attributed to drift, because eight of them showed significant turnover in forest habitats, where the observed community turnover is also higher than expected by drift. Zografou et al. (2014) reported species with significant change in abundance. However, we found that many of these species trends are actually explained by neutral drift, while we found a few more species, not reported by Zografou et al. (2014), whose change in abundance was greater than expected by drift.

The increase of populations of species associated with warm conditions is a frequently observed pattern (Barry et al. 1995; Wilson et al. 2007; Dapporto & Dennis 2013) explained by the northward expansion of species ranges (Parmesan & Yohe 2003). A typical example of a northward range expansion is that of *A. agestis* in Britain (Pateman, Hill, Roy, Fox, & Thomas 2012). The same species increased its abundance significantly in Dadia, unlike in some other Mediterranean areas where its population declined (Stefanescu, Torre, Jubany, & Páramo 2011). Another example of northward range expansion is that of *A. paphia* in northern Europe (Parmesan et al. 1999), a species with significant abundance decline in our study area. Our findings for *A. crataegi* (decreased abundance) are in accordance with corresponding observations from central Spain (Merrill et al. 2008). By contrast,

Table 1. Butterfly species trends in abundance marked with (+): increase or (–): decrease of abundance, for species whose change in abundance is not explained by ecological drift (i.e. species lying outside the 95% confidence intervals in Fig. 2) and for species with significant change in abundance according to a statistical test (reported in Zografou et al. 2014). STI ± SD: Species Temperature Index with ± 1 Standard Deviation (from Schweiger et al. 2014), Habitats: habitats where the species with abundance changes not explained by drift were found (AG = Agriculture, DM = Dry meadow, WM = Wet meadow, GP = Grazed pasture, MF = Mixed forest, OF = Oak forest, PF = Pine forest).

Species names ^a	STI ± SD ^b	Habitats (this study)	Change not explained by drift (this study)	Significant change (Zografou et al. 2014)
<i>Coenonympha pamphilus</i>	8.96 ± 3.89			–
<i>Argynnis paphia</i>	9.02 ± 2.91	MF	–	–
<i>Vanessa cardui</i>	9.04 ± 4.12			–
<i>Polyommatus icarus</i>	9.07 ± 4.11	GP	+	+
<i>Aporia crataegi</i>	9.14 ± 3.53	GP, OF	–	–
<i>Issoria lathonia</i>	9.33 ± 3.08			–
<i>Favonius quercus</i>	9.49 ± 2.79	MF	+	
<i>Maniola jurtina</i>	9.85 ± 3.29	MF	+	+
<i>Thymelicus sylvestris</i>	9.87 ± 2.96			+
<i>Aricia agestis</i>	10.16 ± 2.89	MF, OF, DM	+	+
<i>Satyrium ilicis</i>	10.21 ± 2.91			+
<i>Melitaea didyma</i>	10.42 ± 3.10			+
<i>Hipparchia fagi</i>	10.53 ± 2.62	PF	+	+
<i>Brenthis daphne</i>	10.60 ± 2.90			–
<i>Arethusana arethusana</i>	10.63 ± 2.22			–
<i>Colias crocea</i>	10.69 ± 3.33			+
<i>Melitaea trivia</i>	10.97 ± 2.71			–
<i>Brintesia circe</i>	11.07 ± 2.74			–
<i>Pieris manni</i>	11.46 ± 3.13			–
<i>Argynnis pandora</i>	11.92 ± 3.06	GP	+	
<i>Kirinia roxelana</i>	13.10 ± 2.34	MF, OF, PF	+	+
<i>Hipparchia syriaca</i>	13.13 ± 2.61	PF	+	
<i>Hipparchia fatua</i>	14.03 ± 2.28	DM	+	

^aNomenclature follows updated taxonomy of European Butterflies (Van Swaay et al. 2010).

^bAverage STI of all 88 species sampled is 10.5.

the increased abundance of *Favonius quercus* in our system contrasts with the stable and declining population trends in Catalonia and Andorra (Stefanescu et al. 2011). Finally, the significant increase in abundance of *Maniola jurtina* is in agreement with the prediction of Isaac, Girardello, Brereton, and Roy (2011) for the UK.

The present study is not the first to use a drift model to assess turnover in real communities. Leigh et al. (1993) found that the turnover (over 9 years) of the tree community on the islands of Gatun Lake is not explained by demographic stochasticity, attributing this result to a violent change in environmental conditions. McGill et al. (2005) examined fossil records of mammalian communities across 1 million years and found that they changed less than the neutral drift predicts, concluding that there are also deterministic forces at work in structuring communities. More recently, Dornelas et al. (2014) carried out a meta-analysis of time series from different taxa and geographical regions (with most series concentrated in the last 40 years). They found that the observed community turnover is higher than expected by a neutral model, attributing this to changes of environmental conditions like habitat loss, climate change, species range shifts and invasion. Like Dornelas et al. (2014) we find the observed

community turnover to be higher than expected by the neutral model but the only known systematic change in conditions in our study area is temperature rise, which we consider as the most likely cause of the large turnover.

The method we used assumes that neutral drift is a good approximation to real community drift. However, this assumption is debatable, as many ecologists criticize the neutral model's assumptions. The model ignores interspecific interactions (except for competition for a limited number of resources) and assumes the same fitness for all species; assumptions which we know are not accurate. In the same context, the model ignores butterflies' ecological identity that defines species-specific requirements in terms of habitat use and the microclimatic conditions needed for the viability of its population. Still, the success of a model does not lie in the strict accuracy of its assumptions, but in whether it can reproduce realistic patterns (Rosindell et al. 2012). We will not get into the discussion of how reasonable are the neutral model assumptions. For this the reader may refer to relevant bibliography (e.g. Rosindell et al. 2012; Clark 2012; He, Zhang, & Lin 2012). Based on this discussion, we judge that the model is a good approximation of real drift for relatively large communities for which species differences and interspecific

interactions cancel out and don't affect the average outcome. Although the model's applicability can be limited by its assumptions, it has one great advantage compared to previous models of community drift. That is, it takes into account the sampling effects that arise when localized samples are drawn from a dispersal-limited community. This sampling property extends beyond the model's limits (Etienne & Alonso, 2005) and should be incorporated in statistical inference based on samples.

Our results show that ecological drift can clearly lead to substantial rates of species turnover, rates which could be mistaken for a response to climate change. Furthermore, autocorrelations of environmental variability will substantially increase these rates of turnover. This underlines the need for careful statistical analysis when attributing ecological community changes to climate change or other large-scale processes. In this respect, a null model that simulates ecological drift can be used to exclude the expected natural turnover and thus investigate the causes of any additional turnover. To this end, the neutral model offers a reasonable starting point.

Acknowledgements

We thank the two anonymous reviewers whose suggestions helped improve this manuscript. Vasiliki Sgardeli acknowledges the financial support of A.S. Onassis foundation. Konstantina Zografou acknowledges that data collection in Dadia-Leukimi-Soufli National Park in 2011 has been co-financed by the European Union (European Social Fund – ESF) and Greek national funds through the Operational Program “Education and Lifelong Learning” of the National Strategic Reference Framework (NSRF) – Research Funding Program: Heracleitus II. Investing in knowledge society through the European Social Fund.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2015.12.008>.

References

- Barry, J. P., Baxter, C. H., Sagarin, R. D., & Gilman, S. E. (1995). Climate-related, long-term faunal changes in a California rocky intertidal community. *Science*, *267*, 672–675.
- Chave, J., Muller-Landau, H. C., & Levin, S. A. (2002). Comparing classical community models: Theoretical consequences for patterns of diversity. *The American Naturalist*, *159*, 1–23.
- Clark, J. S. (2012). The coherence problem with the unified neutral theory of biodiversity. *Trends in Ecology & Evolution*, *27*, 198–202.
- Dapporto, L., & Dennis, R. L. H. (2013). The generalist-specialist continuum: Testing predictions for distribution and trends in British butterflies. *Biological Conservation*, *157*, 229–236.
- Devictor, V., Van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., et al. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change*, *2*, 121–124.
- Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., et al. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, *344*, 296–299.
- Etienne, R. S. (2005). A new sampling formula for neutral biodiversity. *Ecology Letters*, *8*, 253–260.
- Etienne, R. S., & Alonso, D. (2005). A dispersal-limited sampling theory for species and alleles. *Ecology Letters*, *8*, 1147–1156.
- Etienne, R. S., & Alonso, D. (2007). Neutral community theory: How stochasticity and dispersal-limitation can explain species coexistence. *Journal of Statistical Physics*, *128*, 485–510.
- Gilbert, B., Laurance, W. F., Leigh, E. G., Jr., & Nascimento, H. E. M. (2006). Can neutral theory predict the responses of Amazonian tree communities to forest fragmentation? *The American Naturalist*, *168*, 304–317.
- Grill, A., & Cleary, D. F. R. (2003). Diversity patterns in butterfly communities of the Greek nature reserve Dadia. *Biological Conservation*, *114*, 427–436.
- Halley, J. M., & Kugiumtzis, D. (2011). Nonparametric testing of variability and trend in some climatic records. *Climatic Change*, *109*, 549–568.
- Halley, J. M., & Iwasa, Y. (2011). Neutral theory as a predictor of avifaunal extinctions after habitat loss. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 2316–2321.
- He, F., Zhang, D.-Y., & Lin, K. (2012). Coexistence of nearly neutral species. *Journal of Plant Ecology*, *5*, 72–81.
- Holbrook, S. J., Russell, J. S., & Stephens, J. S., Jr. (1997). Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecological Applications*, *7*, 1299–1310.
- Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton, NJ: Princeton Univ. Press.
- Isaac, N. J. B., Girardello, M., Brereton, T. M., & Roy, D. B. (2011). Butterfly abundance in a warming climate: Patterns in space and time are not congruent. *Journal of Insect Conservation*, *15*, 233–240.
- Jabot, F., Etienne, R. S., & Chave, J. (2008). Reconciling neutral community models and environmental filtering: Theory and an empirical test. *Oikos*, *117*, 1308–1320.
- Leigh, E. G., Jr., Wright, S. J., Herre, E. A., & Putz, F. E. (1993). The decline of tree diversity on newly isolated tropical islands: A test of a null hypothesis and some implications. *Evolutionary Ecology*, *7*, 76–102.
- McGill, B. J., Hadly, E. A., & Maurer, B. A. (2005). Community inertia of Quaternary small mammal assemblages in North America. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 16701–16706.
- Merrill, R. M., Gutiérrez, D., Lewis, O. T., Gutiérrez, J., Díez, S. B., & Wilson, R. J. (2008). Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. *Journal of Animal Ecology*, *77*, 145–155.
- Meshinev, T., Apostolova, I., & Koleva, E. (2000). Influence of warming on timberline rising: A case study on *Pinus peuce* Griseb. in Bulgaria. *Phytocoenologia*, *30*, 431–438.

- Pamperis, L. N. (2009). *The butterflies of Greece*. Athens: Pamperis Editions.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., et al. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, *399*, 579–583.
- Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*, 37–42.
- Pateman, R. M., Hill, J. K., Roy, D. B., Fox, R., & Thomas, C. D. (2012). Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. *Science*, *336*, 1028–1030.
- Poloczanska, E. S., Brown, C. J., Sydeman, W. J., Kiessling, W., Schoeman, D. S., Moore, P. J., et al. (2013). Global imprint of climate change on marine life. *Nature Climate Change*, *3*, 919–925.
- Robinson, N., Armstead, S., & Bowers, M. D. (2012). Butterfly community ecology: The influences of habitat type, weather patterns, and dominant species in a temperate ecosystem. *Entomologia Experimentalis et Applicata*, *145*, 50–61.
- Rosindell, J., Hubbell, S. P., He, F., Luke, J. H., & Etienne, R. S. (2012). The case for ecological neutral theory. *Trends in Ecology and Evolution*, *27*, 203–208.
- Sagarin, R. D., Barry, J. P., Gilman, S. E., & Baxter, C. H. (1999). Climate-related change in an intertidal community over short and long time scales. *Ecological Monographs*, *69*, 65–490.
- Schweiger, O., Harpke, A., Wiemers, M., & Settele, J. (2014). CLIMBER: Climatic niche characteristics of the butterflies in Europe. *Zookeys*, *367*, 65–84.
- Stefanescu, C., Torre, I., Jubany, J., & Páramo, F. (2011). Recent trends in butterfly populations from north-east Spain and Andorra in the light of habitat and climate change. *Journal of Insect Conservation*, *15*, 83–93.
- Van Swaay, C., Cuttelod, A., Collins, S., Maes, D., López Munguira, M., Šašić, M., et al. (2010). *European red list of butterflies*. Luxembourg: Publications Office of the European Union.
- Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, *85*, 183–206.
- Volkov, I., Banavar, J. R., Hubbell, P., & Maritan, A. (2003). Neutral theory and relative species abundance in ecology. *Letters to Nature*, *424*, 1035–1037.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., et al. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395.
- Wilson, R. J., Gutiérrez, D., Gutiérrez, J., & Monserrat, V. J. (2007). An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology*, *13*, 1873–1887.
- Zografou, K., Kati, V., Grill, A., Wilson, R. J., Tzirkalli, E., Pamperis, L. N., et al. (2014). Signals of climate change in butterfly communities in a Mediterranean protected area. *PLoS ONE*, *9*, e87245. <http://dx.doi.org/10.1371/journal.pone.0087245>

Available online at www.sciencedirect.com

ScienceDirect