Community responses to extreme climatic conditions

Frédéric JIGUET[1*], Lluis BROTONS[2], Vincent DEVICTOR[3]

[1] Centre de Recherches sur la Biologie des Populations d'Oiseaux, UMR 7204 MNHN-CNRS-UPMC, CP 51, Muséum National d'Histoire Naturelle, 55 rue Buffon, F-75005 Paris, France

[2] Biodiversity Department, Forest Technology Centre of Catalonia, Pujada del Seminari, s/n, E-25280 Solsona, Spain

[3] Institut des Sciences de l'Evolution, UMR CNRS-UM2 5554, Université Montpellier 2, F-34095 Montpellier Cedex 05, France

Abstract   Species assemblages and natural communities are increasingly impacted by changes in the frequency and severity of extreme climatic events. Here we propose a brief overview of expected and demonstrated direct and indirect impacts of extreme events on animal communities. We show that differential impacts on basic biological parameters of individual species can lead to strong changes in community composition and structure with the potential to considerably modify the functional traits of the community. Sudden disequilibria have even been shown to induce irreversible shifts in marine ecosystems, while cascade effects on various taxonomic groups have been highlighted in Mediterranean forests. Indirect effects of extreme climatic events are expected when event-induced habitat changes (e.g. soil stability, vegetation composition, water flows altered by droughts, floods or hurricanes) have differential consequences on species assembled within the communities. Moreover, in increasing the amplitude of trophic mismatches, extreme events are likely to turn many systems into ecological traps under climate change. Finally, we propose a focus on the potential impacts of an extreme heat wave on local assemblages as an empirical case study, analysing monitoring data on breeding birds collected in France. In this example, we show that despite specific populations were differently affected by local temperature anomalies, communities seem to be unaffected by a sudden heat wave. These results suggest that communities are tracking climate change at the highest possible rate [*Current Zoology* 57 (3): 406–413, 2011].

Keywords   Bird community, Climate change, Drought, Heat wave, Hurricane

The frequency and intensity of heat waves, droughts and flood storms are strongly associated with patterns of climate change in some areas of the world (Easterling et al., 2000; Archaux and Wolters, 2006). In addition or in parallel to gradual changes in temperature and rainfall, forecasted climate changes are followed by a higher variance in climatic seasonality and hence a higher frequency of extreme climatic events. This could lead to radically different impacts on natural communities in comparison to those deriving from gradual changes such as ongoing global warming. Indeed, contrary to the relatively progressive impacts of the latter, the effects of extreme events on biodiversity are likely to be more difficult to predict (Easterling et al., 2000). They can derive from a combination of both direct effects on biology of a species and indirect sharp modifications of relationships between species and their habitats (Rouault et al., 2006). These mechanisms may lead to abrupt shifts in biodiversity patterns including transitions to new community associations that may not be easy to anticipate (Chase, 2007; Knapp et al., 2008). For instance, climate change and associated increase in extreme climatic events may temporarily push populations and communities to the limits of their adaptive capacity, with possible irreversible shifts (Lavergne et al., 2010). However, the short-term effects of such extreme climatic events might be rapidly compensated if individuals and populations within communities display highly adaptive abilities and/or phenotypic plasticity (Lande, 2009). Beyond the short-term population responses (Johnson and Winkler, 2010), the synchrony and amplitude of population recoveries in local communities might finally determine the extent and severity of the impacts (Schoener and Spiller, 2006).

Here, we first present a brief review of direct and indirect impacts of extreme events on animal communities. Empirical evidence for population and community changes following extreme climatic events are now numerous (see e.g. Parmesan, 2006). Rather than presenting an exhaustive review of this literature we delineate major types of responses generally observed (focusing on the community level) each exemplified by a particular study. While past extreme climatic events can also inform on which species and assemblages have been

affected (e.g. McKinney, 1997), we restricted our approach to contemporary changes easier to relate to ongoing climate modification. We then discuss the potential impacts of an extreme heat wave on local assemblages as an empirical case study, analysing monitoring data on breeding birds collected in France. In this empirical example, we focus on possible changes in community composition associated with the heat wave during summer 2003 (Rebetez et al., 2006).

1 Direct Impacts of Extreme Events on Natural Communities

Direct effects of extreme climatic events such as heat waves and droughts on communities may be derived from the differential impacts on basic biological parameters of individual species, such as mortality or reproductive rates, related to their specific physiological constraints (Easterling et al., 2000). In such cases, communities are expected to undergo rapid shifts towards the dominance of species able to cope with the temperature or water availability constraints imposed by the extreme event. Furthermore, such a sudden disequilibrium can induce irreversible shifts in community composition and structure, potentially considerably modifying the functional traits of the community (Walther, 2010). These shifts are however poorly understood due to the lack of experiments allowing the monitoring of community changes following extreme events across large spatial scales (Knapp et al., 2008). Extreme heat and drought can however provide natural experimental situations in which the effects of an extreme climatic event on the composition of animal communities of different groups can be investigated (Rebetez et al., 2006). For instance, the extremely hot and dry summer in Europe in 2003 reduced the primary productivity of terrestrial ecosystems (Ciais et al., 2005; Archaux and Wolters, 2006), impacted the survival of invertebrate (Rouault et al., 2006) and vertebrate herbivores (Garel et al., 2004) and modified population dynamics of vertebrates of higher trophic levels (Julliard et al., 2004; Jiguet et al., 2006), including increased human mortality (Inserm, 2003[1]). As another example in terrestrial ecosystems, an extreme flood was shown to be responsible for catastrophic species-specific mortality in a desert rodent community, modifying competitive and metapopulation dynamics and resulting in rapid, wholesale reorganization of the community (Thibault

and Brown, 2008). In marine ecosystems, extreme climatic events can surpass a critical thermal boundary triggering abrupt ecosystem shifts seen across multiple trophic levels (Beaugrand et al., 2008), e.g. by provoking mass mortality of some invertebrate communities (Garrabou et al., 2009) or changes in the balance of abundances of vertebrate species (Martinho et al., 2007).

Beyond direct effect on particular communities, extreme climatic events such as droughts and heat waves may also lead to cascade effects on assemblages of different taxonomic groups or guilds (Schoener et al., 2001; Albright et al., 2010). In the Mediterranean, Carnicer et al. (2011) have recently described a widespread crown condition decline in South European forests during 1987–2007. This generalized decline was paralleled by a substantial increase in tree mortality in more xeric areas (Carnicer et al., 2011). In turn, these drought-induced trends have caused a strong dynamic disruption in insect consumer food webs at large spatial scales (entire Iberian Peninsula), producing long-term negative effects (several years of reduced insect population abundances after drought). These results highlight that extreme droughts have induced long-term structural changes in the Mediterranean food webs, possibly increasing the extinction risk of currently endangered species (Carnicer et al., 2011; Stefanescu et al., 2010). Structural community changes caused by multi-trophic interactions have also been reported during a severe drought affecting subalpine habitats in Utah in 1977, and were qualified as an ecological crunch. Indeed, changes in bird guilds were related to profound changes in food resources and water availability: insectivorous birds declined following changes in insect community structure, granivorous species increased because of an exceptional coniferous cone crop, and nectarivorous hummingbirds totally disappeared because of a five week advancement in flower phenology (Smith, 1982). Finally, extreme climatic events can also directly affect basic ecosystem processes (Knapp et al., 2002, 2008). For instance the reported extreme drought-induced trends on plants emerge as a new concern for the conservation of herbivorous communities and associated higher trophic levels (Carnicer et al., 2011; Stefanescu et al., 2010), while hurricanes can alter the entire food-web dynamics of insular ecosystems (Spiller and Schoener, 2007).

---

[1] Inserm, 2003. Impact de la canicule sur la mortalité: les premiers résultats de la mission d'expertise de l'Inserm. Available at http://www.inserm.fr/fr/questionsdesante/dossiers/sante_environnement/att00000579/25septembre2003.pdf.

2   Indirect Impacts of Extreme Events on Natural Communities

However although direct or indirect trophic cascade derived effects of extreme events may be important, they are likely not to be the only ones impacting communities. Extreme events are also likely to impact species and habitats in different radical ways. Species may have more difficulties to track changes in habitat quality derived from changes in the frequency of rare and unpredictable extreme events than from trends in average climatic conditions (Easterling et al., 2000). In fact, by increasing the amplitude of trophic mismatches (e.g. between species and their resources), the increasing impact of extreme events is likely to turn many systems into ecological traps (van de Pol et al., 2010). In a context of increasing impact of extreme events in ecological communities, this effect is likely to be associated with an increasing number of cases in which strong shifts in community structure or a high rate of species loss are expected but not yet measured. The delay with which the community responds to climate changes was coined "climatic debt" with reference to extinction debt concepts (Hanski and Ovaskainen, 2001) in which habitat destruction is predicted to cause time-delayed but deterministic species extinction (Kussari et al., 2009).

Extreme events are also associated with disturbance agents such as storms, hurricanes or fire likely to cause indirect community responses. For instance, hurricanes can greatly increase soil erosion (Madeiros, 2004[2]) or destroy vegetation cover, with subsequent indirect impacts on animal populations and communities because of habitat modifications. For instance, after tropical hurricanes in North and Central America, the immediate deterioration of the vegetation cover has altered the composition of bird communities (Brown et al., 2011). Following this disturbance, nectarivorous and frugivorous species were particularly sensitive, and tended to move to areas where their food resources remained unaltered, although communities seemed to recover towards their original composition rapidly (within a year) (Lynch, 1991; Brown et al., 2011). Therefore, although indirect effects may affect community negatively in some cases, community organization has been reported to be resilient in others (e.g., following hurricanes, Holt, 2006).

In the case of heat waves and droughts, fires are likely to be of utmost importance in areas with high fuel load presence. Recent studies have shown that impacts of fires at the community level are comparable to accumulated climate changes by shifting communities towards early succession species (Clavero et al., 2011). However, the overall impact of a new disturbance regime will depend on the resulting landscape mosaic and the maintenance of refuge areas that can allow species to colonize new areas. Similar studies on birds have also been carried out in areas affected by hurricanes, showing that these produced regional changes in community similarity without significant loss of richness or overall avian abundance (Rittenhouse et al., 2010). These studies have identified several potential mechanisms for these changes in avian diversity, including hurricane-induced changes in forest habitat and the use of refuges by birds displaced from hurricane-damaged forests. Therefore, the prospect of increasing frequency and intensity of extreme climate events such as hurricanes or fires is not necessarily a matter of conservation concern for animals provided that sufficient forest habitats allowing colonization of new suitable areas are maintained within landscapes (Rittenhouse et al., 2010).

A more complex effect of extreme climate events may be identified when climate impact adds up to an already present stressor in the community. Such combined impacts of a hurricane and wildfires have been reported for birds by Lynch (1991). Habitat fragmentation is already considered to be one of the main causes of population decline and species extinction worldwide and could reinforce negative impact of extreme disturbance on communities. For instance, habitat fragmentation can decrease the ability of populations to resist and to recover from environmental disturbances such as extreme weather events. Piessens et al. (2009) investigated how grassland fragmentation affected the impact of the climatically extreme summer on basic biological parameters of a specialist butterfly. Immediately after the summer heat wave, populations of the host plant declined in size, with simultaneous decreases in population size of the herbivore. At the end of the monitoring period, however, most host populations had recovered and only one population went extinct. In contrast, several butterfly populations had gone extinct during the same period, the extinction probability being significantly linked to fragmentation of populations before the heat wave. These results support the prediction that

---

[2] Madeiros J, 2004. The 2004 translocation of Cahow chicks to Nonsuch Island. Bermuda Audubon Society 50th Anniversary Report: 21–23.

specialist species of higher trophic levels are more sensitive to extinction due to the combined impact of habitat fragmentation and severe disturbances (Warren, 2001). Indeed, one expects specialist species to pay a double cost when facing current global changes. First they are more negatively affected than generalists by habitat modifications (Devictor and Robert, 2009). Therefore, they need to track closely the changes in the distributions of their habitat or resources following extreme climatic events.

3　Community Responses and the Neutral Theory

Direct and indirect community responses to extreme climatic events can also be viewed in the light of the neutral versus niche approaches. The neutral theory is based on the simple assumptions that all individuals of all species in a trophically similar community are ecologically equivalent (Hubbel, 2001). From the neutral perspective, the number of species in a community is controlled by species extinction and immigration and by the emergence of new species by speciation and not by deterministic processes. Instead, the niche theory assumes that species interactions are largely determined by the existence of species-specific traits and that community dynamics result from the filtering of species in fluctuating environments according to these traits. Synthesis between these two approaches has recently been proposed (Leibold and McPeek, 2006), while the strengths and weaknesses of particular aspects of each approach is still recurrently debated (Purves and Turnbull, 2010). Measuring community responses to extreme climatic events constitute a useful framework to disentangle the relative importance of neutral and niche-based processes. For instance, one can compare the observed structure and composition of natural communities to the one obtained when simulating the random removal of species. It is likely that the dominance of niche versus neutral processes will depend on the group, scale and severity of the climatic event considered. To our knowledge studies using community response to climate change as an empirical opportunity to confront niche and neutral theories are still missing (Gilman et al., 2010).

4　Heat Wave and Bird Communities: An Empirical Case Study

A severe heat wave affected Western Europe in spring and summer 2003 (Rebetez et al., 2006), and impacted the breeding bird populations of France. Data collected by the national breeding bird survey (Jiguet et al., in press) allowed estimating impacts on reproductive success in 2003 (Julliard et al., 2004) and on 2003–2004 trends in population sizes (Jiguet et al., 2006). These studies were conducted at the species level, and as species were affected differently, depending on their thermal preferences, we should further expect visible effects at the community level. We will also further tackle the eventual differential recovery of populations affected by the heat.

4.1　The French breeding bird survey

Censuses of breeding birds are carried out on randomly selected sites each spring by skilled volunteer ornithologists. Each plot, covering a 2×2 km area, is monitored twice in the spring in order to detect both early and late breeders, before and after 8th May, with 4–6 weeks between the two surveys. In each square, observers carry out 10 evenly distributed point counts (separated by at least 300 m), where every individual bird, heard or seen, is recorded during a five minutes survey. For a given site, counts are repeated yearly by the same observer at the same points, on approximately the same date (± 7 days during April to mid-June), and at the same time in the day (± 15 min). For each point, the maximum counts per species between the two sessions are retained and summed for the 10 points of a square as a measure of local species abundances.

4.2　Local trend in the community temperature index

To estimate the change in composition of bird communities following temperature change, we used a method already extensively described by Devictor et al. (2008). In brief, we characterized bird communities in sample sites by their community temperature index (CTI) for each year from 1990 to 2008. The CTI is a simple means to measure the rate of change in community composition in response to temperature change. It is calculated, for a given species assemblage, as the average of each Species Temperature Index (STI) occurring in this assemblage, weighted by species abundance. The STI of a given species is the long-term average temperature over the species' range (Jiguet et al., 2010). It is calculated as the temperature of the reproductive season (i.e. March to August) averaged across the species distribution of an area of interest. STIs were obtained for birds from the combination of the distribution in (March–August) European temperature and the atlas of European breeding birds (Hagemeijer et al., 1997). STI was shown to be a powerful proxy for the thermal

niche centre of the species and has been validated as a straightforward niche metric to predict short (Jiguet et al., 2006) and long-term responses (Jiguet et al., 2007) of breeding bird species to climate change.

A temporal increase in CTI (°C per year) directly reflects that the relative abundance of individuals belonging to species dependent on higher temperatures (i.e. with a high STI) is increasing within species assemblages. During 1990–2008, CTI increased steeply suggesting a consistent change in community composition towards hot-temperature dwellers (Devictor et al., 2008). But beyond the long-term trend in CTI at the national level, whether punctual and local extreme heat wave is followed by changes in local CTI is unknown. Here, the yearly change in CTI was calculated on 1996 sites using breeding bird survey data for 217 species to investigate whether beyond the average increase in CTI, local communities have responded to an unprecedented climatic event, i.e. the very hot spring and summer 2003. We first estimated how the relative change in CTI for the year 2003 varied across sites compared to other years in the 1989–2008 period following Julliard et al. (2004). To do so, we used a categorical variable separating 2003 from other years (Y2003). Among site variation in CTI was tested from the model CTI ~Site+Site: Y2003. In this model, the interaction term provides an estimate of relative changes in CTI for the year 2003 in each site accounting for among site variation in CTI. Using simple regression, this estimate was further related to site-specific temperature in 2003 during the breeding season (obtained from Météo-France, 2005[3]). This model allows investigating whether local change in CTI was dependent on the local temperature in 2003. The same relationship was tested using local temperature anomaly instead of temperature *per se*.

At the country scale, 2003 clearly represented a year with exceptional temperature increase since 1950 or even since 1989 when a consistent increase in temperature occurred in France (Fig. 1). On average, the CTI in 2003 was not higher than in previous years (effect of the year 2003 on average CTI: $F_{1, 3124} = 0.80$, $P = 0.36$). However, at the scale of local sites, the increase in local CTI was larger in hotter sites (effect of local average temperature on local increase in CTI $F_{1, 646} = 9.53$, $P = 0.002$, slope $\pm SE = 0.011\pm0.003$). This effect reveals that local increase in CTI was not randomly distributed in space but was higher in southern France. However, this local increase in CTI could not be interpreted as a

particular local adjustment to the extreme temperature anomalies in 2003. Indeed we found no evidence for a relationship between local increase in CTI and local temperature anomaly (effect of 2003 summer temperature anomaly on local increase in CTI from 2003 to 2004: $F_{1, 646} = 0.99$, $P = 0.31$; see Fig. 2). In other words, the consistent and linear increase in CTI of the French avifauna documented in Devictor et al. (2008) is probably occurring at its higher rate with no potential acceleration for extra community adjustment to a particularly high temperature in a given year. Obviously, this adjustment could be delayed if populations do not respond instantaneously to climate change. However, we found no evidence for extra increase in CTI for the year 2004 or for the relative change in CTI between 2003 and 2004 ($F_{1, 646} = 0.46$, $P = 0.49$; and $F_{1, 646} = 1.25$, $P = 0.26$ respectively). However, some further tests revealed some trends in the variance of the response of the community index to the local temperature anomaly during the heat wave. A Bartlett's test for variance homogeneity (K = 56, $P < 0.0001$) suggest that the variance in CTI was unevenly distributed along the temperature anomaly gradient (Fig. 2). The larger the temperature anomaly, the more similar the change in CTI across sites. This means that the response seems to be forced, constrained by anomalous high temperatures. This result is however not maintained in a more robust approach using a Levene's test (Levene's statistic = 1.06, $P = 0.14$). Overall, this result shows that the average composition of the community was not modified by the heat and its intensity, despite identified effects for individual species (Jiguet et al., 2006): hot- or cold-dwelling species have not been affected sufficiently to change metrics obtained at the community level.

These results suggest that communities are tracking gradual change in temperature but that, beyond this change, communities have no further ability to adjust to an extreme local temperature change. However, the absence of community changes in a given year may mask important changes in populations of individual species. More detailed investigations on species by species responses to climate change are therefore needed to highlight which species are more at risk, where, and why.

4.3   Local potential recovery of impacted populations

To estimate the potential recovery of bird populations we further used a species-by-species approach. From the

---

[3] Météo-France, 2005. Retour sur la canicule. Available at: http://www.meteofrance.com/FR/actus/dossier/archives/canicule2003/dos.htm
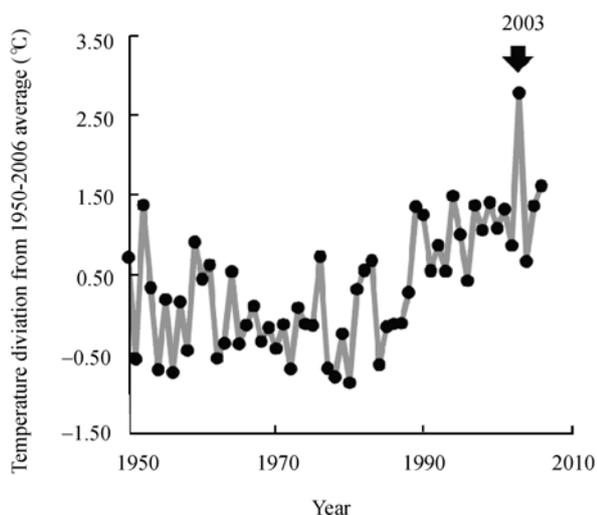
Fig. 1 Long-term trends in spring and summer (March–August) temperature anomaly in France since 1950
Temperature anomaly is calculated as the difference from the mean temperatures during 1961–1990.
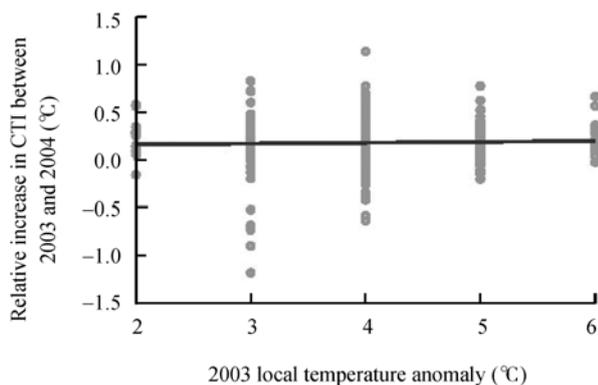

Fig. 2 Response of the Community Temperature Index to the summer temperature anomaly following the 2003 heat wave
The regression line is shown.

breeding bird survey data, changes in population sizes of each species are estimated with Poisson regression using abundance as the dependent factor, first accounting for a site effect and then testing for a year effect as a factor. Resulting estimates of national population indices are stored for 86 species for the period 2002–2009 for which trends can be reliably estimated. Year-to-year changes in population sizes are estimated for each pair of successive years by dividing the index of year (x+1) by the index of year (x). We further looked for correlation coefficients between successive pairs of years, expecting significant negative correlations due to either population re-equilibrium or random distribution of sampling variance, or both: the probability of facing a

decrease after an increase, or inversely, should therefore lead to significant correlation between population growth rates of successive years. Accordingly, we found that all successive pairs of index changes are significantly and negatively correlated (r = -0.29 to -0.46, all P < 0.006) except for the comparison between the pairs of years 2003-2004 and 2004-2005 (r = -0.13, df = 5, P = 0.22). This suggests that there was no re-equilibrium of population sizes after the strong impact of the heat wave. Specific populations did not seem to be able to recover rapidly in terms of population density from the negative impact of the heat wave. The short-term recovery of bird populations of individual species seems to be the rule except after a strong impact of extreme high temperatures. The non-recovery of breeding populations impacted by the heat wave inevitably implies changes in local community composition, which are however not visible when calculating the instantaneous change in CTI.

5 Conclusion

Overall, extreme events and interactions between extreme events and different components of global change are likely to cause a range of unknown new pressures and constraints on ecological communities. The major prediction is that biodiversity impacts from these effects are likely to markedly differ from those resulting from common gradual climate change (Walther, 2010). Interactions between such extreme events and other ongoing rapid human-induced drivers of global changes are likely to create unprecedented and unpredictable stressful environmental conditions for species, especially those with lower movement capacities and dispersal abilities. In this context, we predict a loss of specialist species in areas more subjected to extreme climatic events, especially in areas where extreme climatic events interact with global change components such as changes in land use, perturbation regimes or the presence of introduced invasive species. This seems to be coherent with the larger increase in CTI in Mediterranean southern France during the 2003 heat wave, as terrestrial Mediterranean biodiversity is under strong habitat change pressures (Clavero et al., 2011). In any case, the incorporation of extreme events on the predicted impacts of global change for communities is likely to become a critical issue in the future (Knapp et al., 2008; Zimmermann et al., 2009). Using both long and short term changes in both community structures and population sizes may help to improve our ability to monitor this issue for different taxonomic groups across

trophic levels.

Finally, studying reaction norms, changes and adaptations in communities located in the most unpredictable environments on Earth may inform about the mechanisms of plasticity that are able to provide an adaptive response to climatic extremes (Canale and Henry, 2010). As climate changes cause climatic hazards, these resilience mechanisms are expected to spread within species, populations and communities (Lavergne et al., 2010). As an illustration, evidence from long-term studies of species assemblages under strong El Niño Southern Oscillation influence, e.g. Darwin finches on the Galapagos Islands (Grant et al., 2000), should bring valuable information on relative species and hence community resilience. For these species, extreme climatic events are not extra-niche conditions: populations within such communities are likely to have been selected to be adaptive over very large climatic gradients including frequent extreme events, compared to organisms from currently stable, temperate climates. Communities living in highly variable or seasonal environments may help with refining forecasts of the future of communities facing increasing extreme climatic events.

References

Albright TP, Pidgeon AM, Rittenhouse CD, Clayton MK, Flather CH et al., 2010. Effects of drought on avian community structure. Glob. Change Biol. 16: 2158–2170.

Archaux F, Wolters V, 2006. Impact of summer drought on forest biodiversity: What do we know? Ann. For. Sci. 63: 645–652.

Beaugrand G, Edwards M, Brander K, Luczak C, Ibanez F, 2008. Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. Ecol. Lett. 11: 1157–1168.

Brown DR, Sherry TW, Harris J, 2011. Hurricane Katrina impacts the breeding bird community in a bottomland hardwood forest of the Pearl River basin, Louisiana. For. Ecol. Manage. 261: 111–119.

Canale CI, Henry PY, 2010. Adaptive phenotypic plasticity and resilience of vertebrates to increasing climatic unpredictability. Clim. Res. 43: 135–147.

Chase JM, 2007. Drought mediates the importance of stochastic community assembly. PNAS 104: 17430–17434.

Carnicer J, Coll M, Ninyerola M, Pons X, Sánchez G et al., 2011. Widespread crown condition decline, food web disruption and amplified tree mortality with increased climate-change-type drought. Proc. Natl. Acad. Sci. USA. 108(4): 1474–1478.

Ciais P, Reichstein M, Viovy N, Granier A, Ogée J et al., 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437: 529–533.

Clavero M, Brotons L, Villero D, 2011. Climate change or land use dynamics: Do we know what climate change indicators indicate? PLoS ONE (in press)

Devictor V, Julliard R, Couvet D, Jiguet F, 2008. French birds lag behind climate warming. Proc. R. Soc. Lond. B 275: 2743–2748.

Devictor V, Robert A, 2009. Measuring community responses to large-scale disturbance in conservation biogeography. Div. Distrib. 15: 122–130.

Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR et al., 2000. Climate extremes: observations, modeling, and impacts. Science 289: 2068–2074.

Garel M, Loison A, Gaillard J-M, Cugnasse J-M, Maillard D, 2004. The effects of a severe drought on mouflon lamb survival. Proc. R. Soc. Lond. B 27: S471–S473.

Garrabou J, Coma R, Bensoussan N, Bally M, Chevaldonné P et al., 2008. Mass mortality in Northwestern Mediterranean rocky benthic communities: Effects of the 2003 heat wave. Glob. Change Biol. 15: 1090–1103.

Gilman S, Urban M, Tewksbury J, Gilchrist G, Holt R, 2010. A framework for community interactions under climate change. Trends Ecol. Evol. 25: 325–331.

Grant PR, Grant BR, Keller LF, Petren K, 2000. Effects of El Niño events on Darwin's finch productivity. Ecology 81: 2442–2457.

Hagemeijer WJM, Blair MJ, 1997. The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. London, UK: T & AD Poyser.

Hanski I, Ovaskainen O, 2001. Extinction debt at extinction thresholds. Conserv. Biol. 16: 666–673.

Holt RD, 2006. Making a virtue out of a necessity: Hurricanes and the resilience of community organization. Proc. Natl. Acad. Sci. USA 103: 2005–2006.

Hubbell SP, 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton: Princeton University Press.

Jiguet F, Julliard R, Thomas CD, Dehorter O, Newson SE et al., 2006. Thermal range predicts bird resilience to extreme temperatures. Ecol. Lett. 9: 1321–1330.

Jiguet F, Gadot A-S, Julliard R, Newson SE, Couvet D, 2007. Climate envelope, life history traits and the resilience of birds facing global change. Glob. Change Biol. 13: 1672–1684.

Jiguet F, Gregory RD, Devictor V, Green RE, Vorisek P et al., 2010. Population trends of European birds are correlated with characteristics of their climatic niche. Glob. Change Biol. 16: 497–505.

Jiguet F, Devictor V, Julliard R, Couvet D (in press) French citizens monitoring ordinary birds provide tools for conservation and ecological sciences. Acta Oecologica.

Johnson AB, Winkler K, 2010. Short-term hurricane impacts on a neotropical community of marked birds and implications for early-stage community resilience. PLoS ONE 5(11): e15109.

Julliard R, Jiguet F, Couvet D, 2004. Evidence for impact of global warming on common birds population long term dynamics. Proc. R. Soc. Lond. B (Suppl.) S490–S492.

Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD et al., 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298: 2202–2205.

Knapp AK, Beier C, Briske DD, Classen AT, Luo Y et al., 2008.

Consequences of more extreme precipitation regimes for terrestrial ecosystems. Bioscience 58(9): 1–11.

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J et al., 2009. Extinction debt: A challenge for biodiversity conservation. Trends Ecol. Evol. 24: 564–571.

Lande R, 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. J. Evol. Biol. 22: 1435–1446.

Lavergne S, Mouquet N, Thuiller W, Ronce O, 2010. Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. Ann. Rev. Ecol. Evol. Syst. 41: 321–350

Leibold MA, McPeek, MA, 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87: 1399–1410.

Lynch JF, 1991. Effects of hurricane Gilbert on birds in a dry tropical forest in the Yucatan Peninsula. Biotropica 23: 488–496.

Martinho F, Leitão R, Viegas I, Dolbeth M, Neto JM et al., 2007. The influence of an extreme drought event in the fish community of a southern Europe temperate estuary. Estuar. Coast. Shelf Sci. 75: 537–546.

McKinney ML, 1997. Extinction vulnerability and selectivity: Combining ecological and paleontological views. Annu. Rev. Ecol. Evol. Syst. 28: 495–516.

Parmesan C, 2006. Ecological and Evolutionary Responses to Recent Climate Change. Annu. Rev. Ecol. Evol. Syst. 37: 637–69.

Piessens K, Adriaens D, Jacquemyn H, Honnay O, 2009. Synergistic effects of an extreme weather event and habitat fragmentation on a specialised insect herbivore. Oecologia 159: 117–126.

Purves DW, Turnbull LA, 2010. Different but equal: The implausible assumption at the heart of neutral theory. J. Anim. Ecol. 79: 1215–1225.

Rebetez M, Mayer H, Dupont O, Schindler D, Gartner K et al., 2006. Heat and drought 2003 in Europe: A climate synthesis. Ann. For. Sci. 63: 569–577.

Rittenhouse CD, Pidgeon AM, Albright TP, Culbert PD, Clayton MK et al., 2010. Avifauna response to hurricanes: Regional changes in community similarity. Glob. Change Biol. 16: 905–917.

Rouault G, Candau JN, Lieutier F, Nageleisen L-M, Martin J-C et al., 2006. Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. Ann. For. Sci. 63: 613–624.

Schoener TW, Spiller DA, Losos JB, 2001. Predators increase the risk of catastrophic extinction of prey populations. Nature 412: 183–186.

Schoener TW, Spiller DA, 2006. Nonsynchronous recovery of community characteristics in island spiders after a catastophic hurricane. Proc. Natl. Acad. Sci. USA 103: 2220–2225.

Smith KG, 1982. Drought-induced changes in avian community structure along a montane sere. Ecology 63: 952–961.

Spiller DA, Schoener TW, 2007. Alteration of island food-web dynamics following major disturbance by hurricanes. Ecology 88: 37–41.

Stefanescu C, Carnicer J, Peñuelas J, 2010. Determinants of species richness in generalist and specialist Mediterranean butterflies: The negative synergistic forces of climate and habitat change. Ecography. doi: 10.1111/j.1600–0587.2010.06264.x

Thibault KM, Brown JH, 2008. Impact of an extreme climatic even ton a community assembly. Proc. Natl. Acad. Sci. USA 105: 3410–3415.

Van de Pol M, Ens BJ, Heg D, Brouwer L, Krol J et al., 2010. Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? J. Appl. Ecol. 47: 720–730.

Walther G-R, 2010. Community and ecosystem responses to recent climate change. Phil. Trans. R. Soc. B 365: 2019–2024

Warren MS, Hill JK, Thomas JA, Asher J, Fox R et al., 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414: 65–69.

Zimmermann NE, Yoccoz NG, Edwards TC Jr, Meier ES, Thuiller W et al., 2009. Climatic extremes improve predictions of spatial patterns in tree species. Proc. Natl. Acad. Sci. USA 106: 19723–19728.