

4. From Phosphorus and VOCs to Biodiversity: Some Studies on the Effects of Global Change Inspired by Margalef's Legacy

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4.1. Introduction

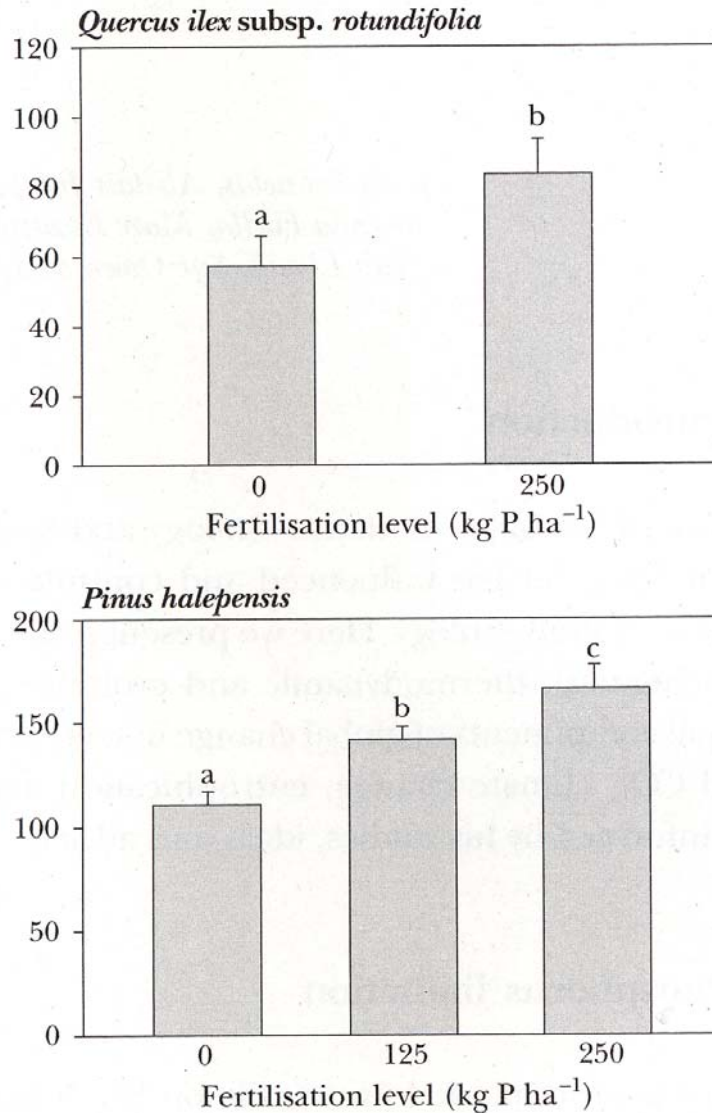
The work of Margalef in marine biology and limnology is well known, but Margalef has influenced and continues to influence the field of terrestrial ecology. Here we present some recent results on biogeochemical, thermodynamic and evolutionary aspects of the principal components of global change in terrestrial ecosystems (increased CO₂, climate change, eutrophication and changes in land use) informed by his studies, ideas and advice.

4.2. Phosphorus limitation

Margalef often reminded us that life on Earth has phosphorus as a limiting chemical element and that *one of the major deficiencies of terrestrial ecology is the lack of information on phosphorus*. Considerable efforts have been made in recent years to try to remedy this lack of knowledge about phosphorus in terrestrial ecosystems. Indeed, we have observed how this limitation is present in many terrestrial systems. Figure 4.1 shows an example in Mediterranean pine trees on limestone soils (Sardans, Roda and Peñuelas 2004).

We are now seeing how one of the major environmental changes, the increase in atmospheric CO₂, perhaps the paradigm of global change generated by man and his activities in the last few centuries, in some cases accentuates this limitation. Figure 4.2 shows an example of how the foliar concentration of phosphorus

FIGURE 4.1: Mean effects (+ S.D.) of phosphorus fertilisation on relative height growth of naturally-regenerated *Pinus halepensis* saplings, and of *Quercus ilex* subs. *rotundifolia* resprouts 5 years after fire



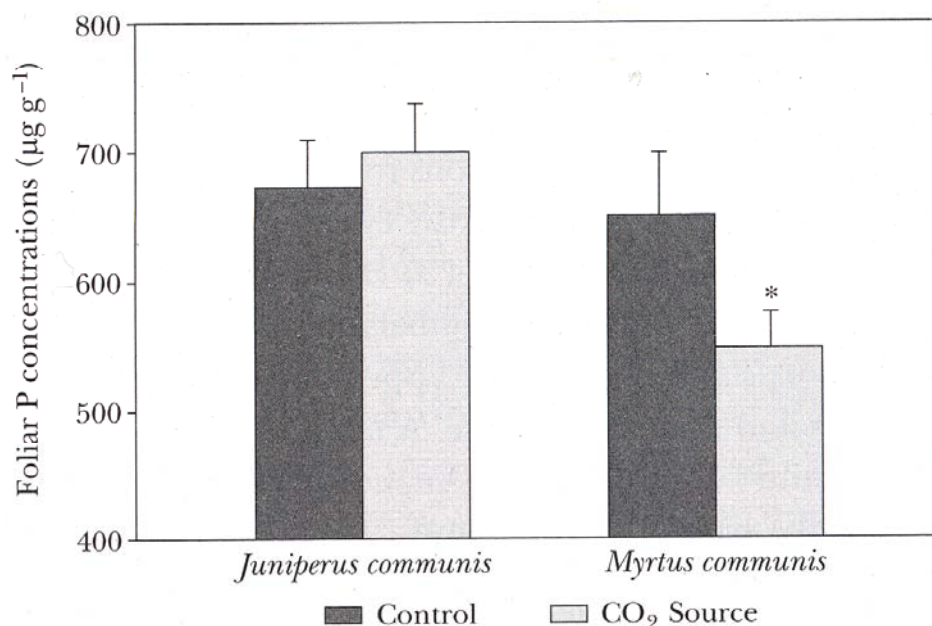
Note: The results are calculated three years after fertiliser application in a field experiment. Different letters indicate significantly different values ($p < 0.05$) for the different p fertilisation levels in a Duncan new multiple range post-hoc test.

Source: Modified from Sardans, Roda and Peñuelas (2004).

decreases in the plants of some species when they are subjected to high concentrations of CO₂ while other species appear not to be affected (Peñuelas, Filella and Tognetti 2001). In this way, new, competitive capabilities develop and, with them, the possibility for changes in communities.

Another of the major environmental changes, global warming, associated with drought in Mediterranean ecosystems, also reduces

FIGURE 4.2: Concentrations of phosphorus in leaves of plants from two species



Note: Plants grown at different distances from a CO₂ source, with mean CO₂ concentrations of 380 and 700 µmol mol⁻¹. Error bars are SEM ($n = 36$) * $p < 0.05$, ANOVA.

Source: Modified from Peñuelas, Filella and Tognetti (2001).

the availability of phosphorus. Sardans and Peñuelas (2005) and Sardans, Peñuelas and Estiarte (2007) have observed how the activity of root and soil phosphatases decreases under experimental conditions that simulate the drought predicted for the next few decades in the Mediterranean region (a reduction of 15-20% in soil humidity; see IPCC 2001; Sabater, Gracia and Sanchez 2002; Peñuelas et al. 2004). In fact, fungal activity reduces quickly with drought, and an example of this is the lower biomass of mushrooms in plots subjected to a 15-20% reduction in soil humidity in these experimental systems (Ogaya and Peñuelas 2005). The overall result is a fall in inorganic phosphorus available for plants, thus making it yet more limiting (Sardans and Peñuelas 2004).

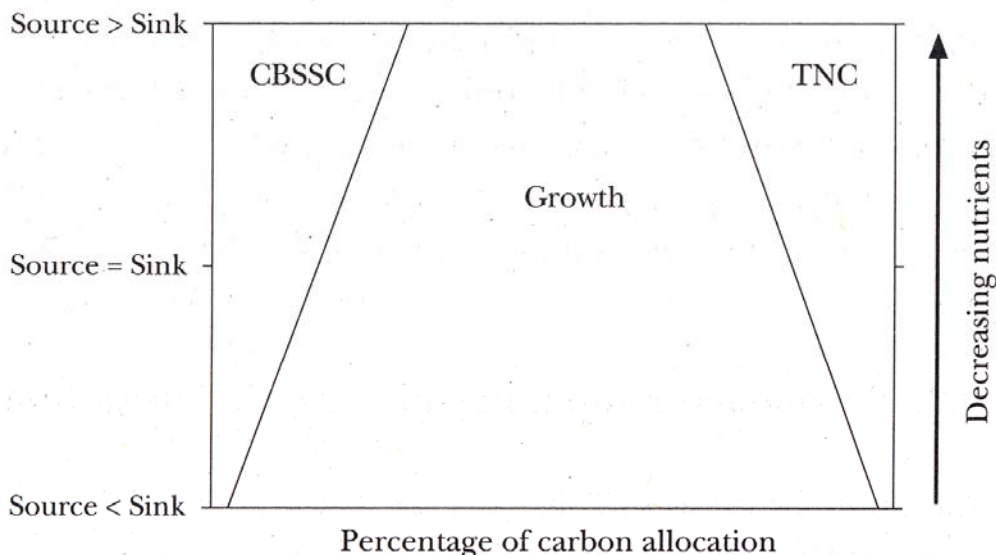
4.3. Secondary compounds that are rich in carbon

Although synthesis of living matter is not possible when there is a lack of nutrients such as phosphorus or nitrogen, the photosynthetic system, whilst it continues to receive light, does not

stop creating reducing power for the cell and this even increases as CO_2 levels rise. The synthesis of organic material is therefore uninterrupted and additional carbon may be assigned to secondary, carbon-rich compounds that are difficult to digest or decompose (phenolic compounds, tanins, celluloses, lignins, isoprenoids, etc.); this has important implications for the relationship with herbivores and decomposers and for the cycle of matter, and thus, for planetary biogeochemistry (figure 4.3) (Peñuelas and Estiarte 1998).

On a different timescale, this imbalance is also important from an evolutionary standpoint for the appearance of wood and, therefore, of trees and their dominance. A taller tree with deeper roots has a competitive advantage over smaller plants; this enables us to understand the type of life and landscape we have on our planet. Margalef, with imaginative foresight (Margalef 1997), interpreted the appearance of wood as consecutive to the synthesis of its principal components, classified basically into groups of celluloses and lignins, as a consequence of phosphorus-induced limitation and the capacity of photosynthesis to continue to create reducing power for the cell as long as it receives light.

FIGURE 4.3: The excess carbon generated by the continuing work of the photosynthesising system when growth reduces due to lack of nutrients ends up allocated to carbon-based secondary compounds like, for example, phenolic compounds and non-structural carbohydrates



Source: Modified from Peñuelas and Estiarte (1998).

4.4. Volatile organic compounds

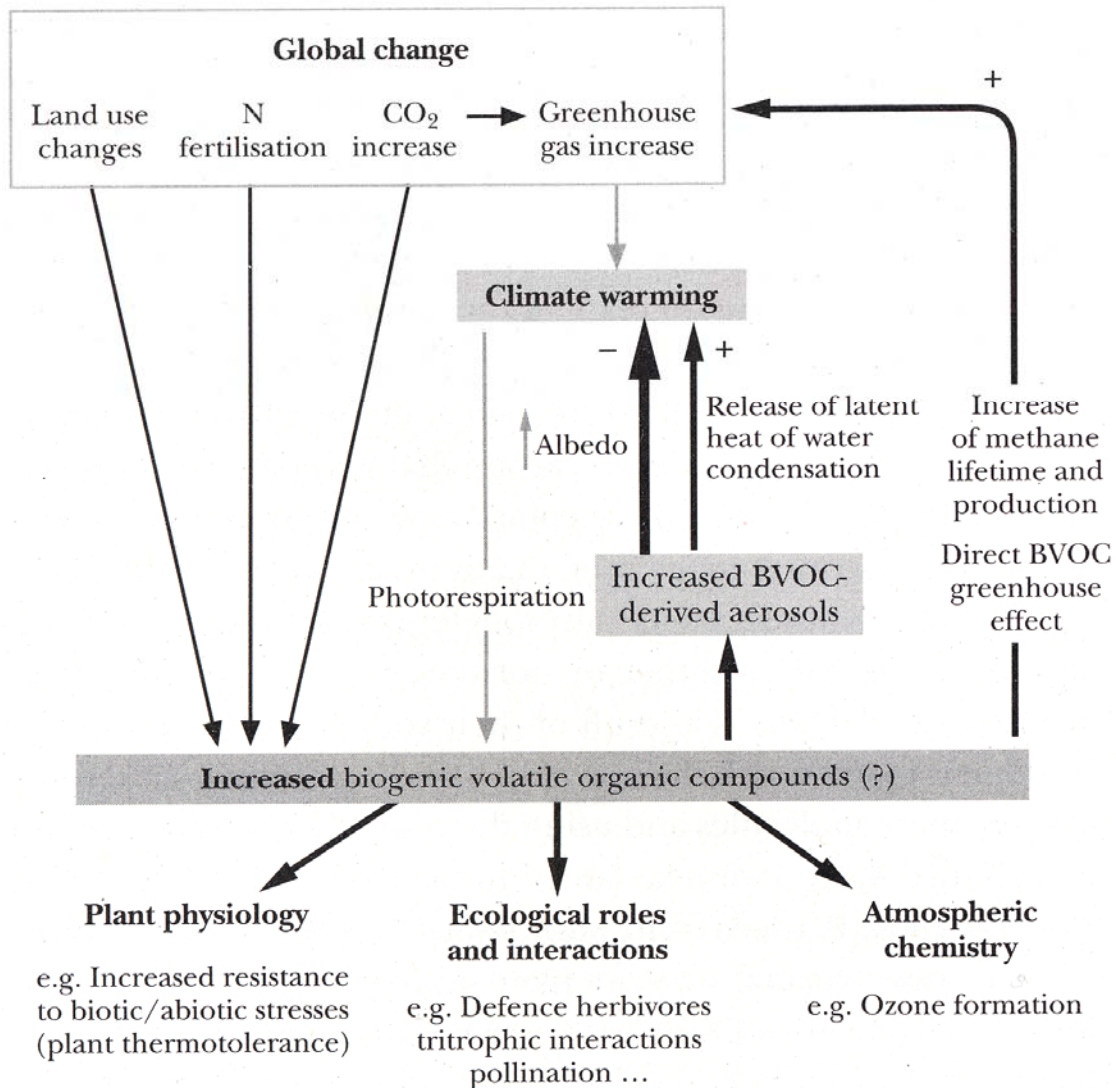
Plants produce a great diversity of these carbon-rich organic compounds and some, indeed many of them, are volatile. Given that their emission is inevitable as a result of this volatility, we have taken inspiration from Margalef to establish the hypothesis that there does not necessarily have to be a specific role for each volatile organic compound (VOC) that is emitted. As Margalef reminds us, the result of the events and experiments of life is a gradual and cumulative increase in the complexity of nature over time. This increasing complexity is also the cause of the diversity of the VOCs that are emitted by plants, often with no apparent function, representing a loss of carbon that is apparently negative for the plant. For some of these compounds, evolution has turned this possible inconvenience into an advantage by using them, for example, as metabolic safety valves, defences, protection or communication signals. Whether or not they have an adaptive role, the emission of VOCs is a result of their volatility. What evolution has done is to work with the inevitable, finding physiological functions for these molecules and using them to relate to other organisms (figure 4.4) (Peñuelas and Llusà 2003, 2004; Owen and Peñuelas 2005; Peñuelas and Munné-Bosch 2005).

In any case, what we have are plant emissions of volatile organic compounds that are tending to increase as a consequence of global change. This increase is altering relationships between plants and other organisms (pollinators, herbivores, herbivore predators and parasitoids, other plants, microorganisms...) and protective functions against excess radiation, excess temperature, oxidation, etc. Finally, these changes in VOC emissions affect the atmospheric concentration of secondary contaminants such as ozone, and appear to have both negative and positive biofeedback effects on climate (Peñuelas and Llusà 2003).

4.5. Climate change

Although these changes in volatile organic compounds and, in general, in the carbon-rich secondary compounds, appear to be of

FIGURE 4.4: Effects of the components of global change on the emission of volatile organic compounds (VOCs) and their biological, environmental and feedback roles on climate



Source: Modified from Peñuelas and Llusà (2003).

considerable importance and are doubtless worthy of our scientific attention, there are other biological changes directly related to the global environmental changes that we are experiencing which can have a more direct effect on species function and interactions. Among the most important is climate change.

We know that interannual variability in the climate is normal even in the absence of long-term climate changes. We also know that organisms and species are capable of tolerating this short-term variability by means of phenotypic plasticity. One example is the spectacular phenological changes that have occurred over the past

few decades, with earlier leafing and blooming; this is of major importance for the function of ecosystems and the biosphere and for the composition of communities, given the changes in the competitive capacities that result from the failure of response synchrony (Peñuelas and Filella 2001a; Peñuelas, Filella and Comas 2002). Although organisms may be capable of modifying their phenology, they frequently react to the onset of suboptimal climatic conditions by reducing their activity and productivity. This has occurred for example in lower altitude areas of the Montseny mountains, where beech trees are growing 49% less than in the period 1952-1975, when the temperature was 1.65 °C lower, with consequently lower evapotranspiration and aridity (Jump, Hunt and Peñuelas 2007).

The next step in species' response to climate change is adaptation, genetic change. In fact, many studies using molecular markers have demonstrated that microgeographical genetic differentiation within populations correlates with numerous climatic factors. It is therefore distinctly possible that we have underestimated the role of adaptation as a response to the current climate change (Jump and Peñuelas 2005). It now seems that even in a relatively small forest such as that found in the Montseny mountains, typically distributed at an altitude between 1000 and 1700 metres, beech trees at higher altitudes can be distinguished from those lower down at certain loci, demonstrating that a selection process is at work, associated with the increase in temperature (Jump et al 2006). In fact, a positive relationship has been observed at higher altitudes between the number of new beech trees recruited and the temperature, which turns negative at lower altitudes (Jump, Hunt and Peñuelas 2007).

In any event, numerous studies show that the rate of evolution (adaptation) cannot keep up with the speed of climate change (Jump and Peñuelas 2005) and that species eventually respond by shifting to habitats with more suitable climatic conditions. This has occurred in the Montseny area (Peñuelas and Boada 2003) and in many other sites (Walther et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). Overall, these studies have documented a mean poleward shift of 6.1 km per decade or of 6.1 metres per decade towards higher altitudes (Parmesan and Yohe 2003).

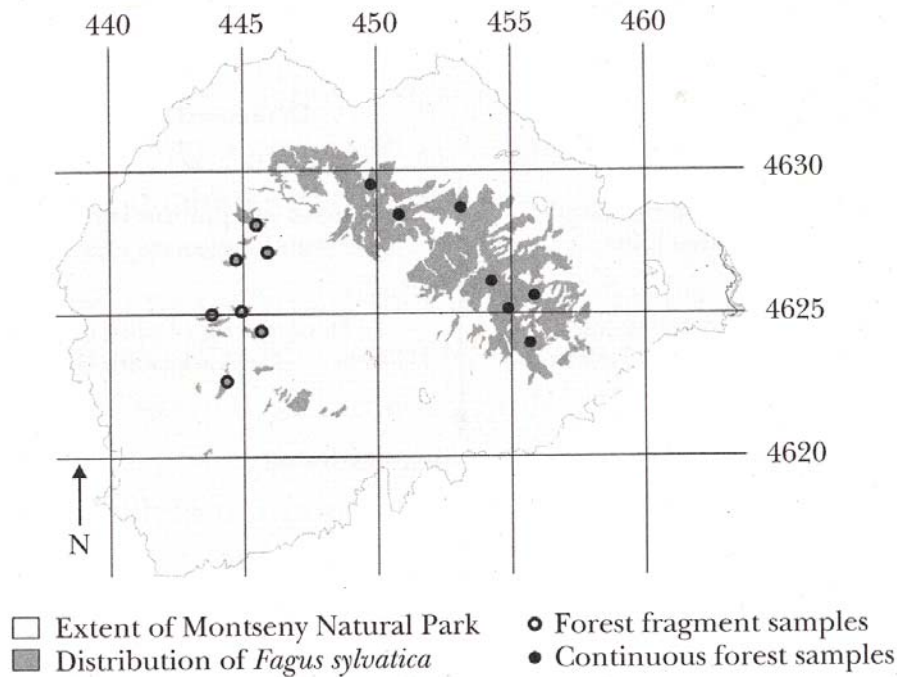
4.6. Other components of global change

Biological responses to global change are complex, because the components of this change also interact and are separated in turn by spatial and temporal differences. For example, current environmental changes may not only accelerate the limiting role of certain nutrients, as we have seen above. Conversely, human beings are in many cases fertilising the planet. In fact, eutrophication was one of the first words that Margalef pronounced as a magical prelude to his general biology classes. Those of us who had him as ecology professor will recall that the first exam Margalef set in 1976 for his first-year general biology students had a question on: *Eutrophication*. As in so many other questions, Margalef was ahead of his time in recognising one of the major environmental changes now affecting ecosystems, including the terrestrial ecosystems of the Mediterranean area (Peñuelas and Filella 2001b).

4.7. Changes in land use: fragmentation

Atmospheric changes, climate change, eutrophication and loss of biodiversity are among the global anthropogenic disturbances that Margalef examined from his particular viewpoint; but he did not neglect that other key component of global change, the transformation of land use. Keenly interested in the dynamic topology of the landscape, in the last years of his life he studied the transformation of Spain in particular and the planet in general. Just a few decades ago, our territory was relatively natural, little travelled and dotted with a few nuclei inhabited by humans. Now it is full of inhabited nuclei and roads along which vehicles and information pass, and our own species is leaving less and less space for other species to survive. These considerations also find an interesting expression in the magnificent natural laboratory of Montseny. To our surprise, we found that fragmentation occurring several centuries ago (see figure 4.5) had had a profound effect on the reproductive system of the beech, giving rise to high inbreeding rates, high populational divergence and reduced genetic diversity within isolated populations. This had occurred despite the beech being

FIGURE 4.5: Continuous and fragmented beech forestry mass in the Montseny mountains



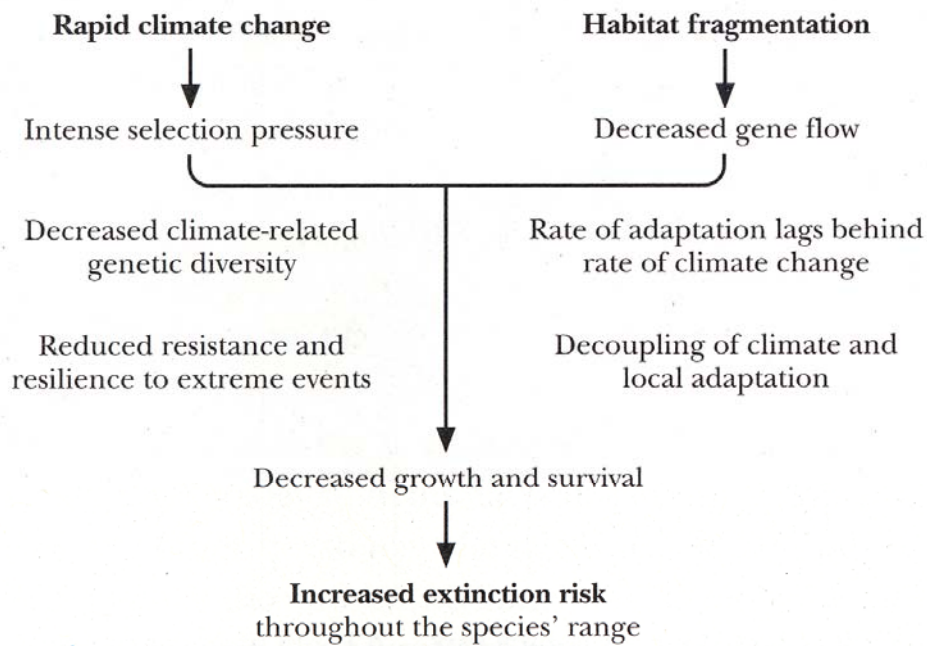
Note: The lines correspond to UTM (Universal Transverse Mercator) coordinates in km. Fragments are twice as inbred, exhibit three times more genetic differentiation and have lost nearly five times more rare alleles than the continuous forestry mass.

Source: Modified from Jump and Peñuelas (2006).

an anemophilous tree and the fact that the fragments were so close to one another (separated by distances of 1-6 km) (Jump and Peñuelas 2006). This finding shows that trees, despite their relatively long life, are not exempt from the risks of environmental change, and has important implications for the management of natural and seminatural spaces.

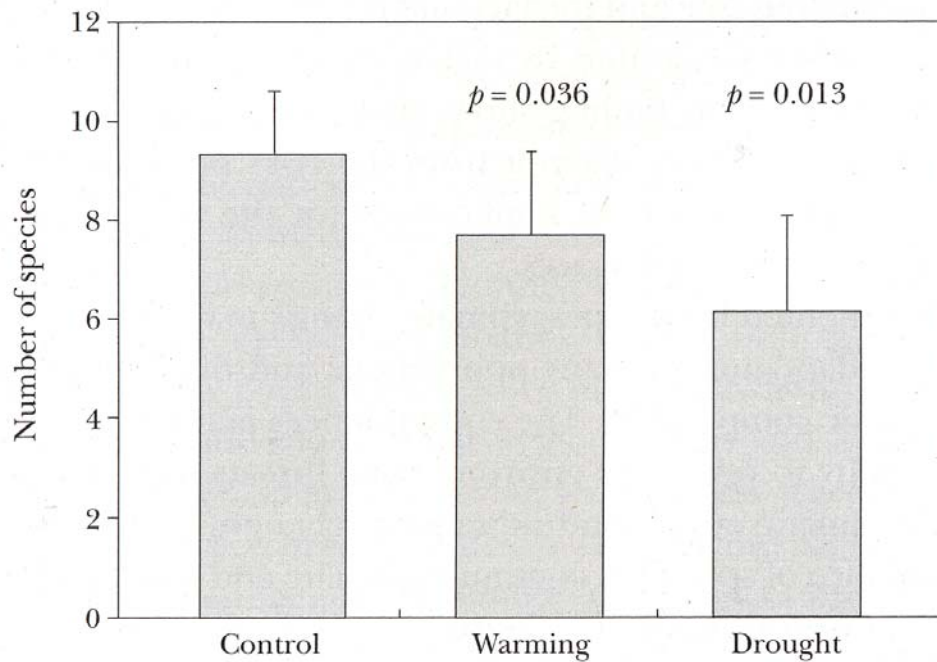
In fragmented landscapes, climate change may exceed the capacity of adaptation in many populations and dramatically alter their genetic composition. The consequences may include an impaired ability to resist new environmental threats such as pests or extreme climatic events, and subsequent changes in the presence or abundance of species in communities. The end result is that the risk of extinction increases (figure 4.6). In fact, in experimental studies where we simulated the warming and drought conditions predicted for the next few decades in the shrublands of Garraf (Barcelona), we observed that there was a reduction in the number of species recruited (figure 4.7) (Lloret, Peñuelas and Estiarte 2004).

FIGURE 4.6: Interaction between climate change and fragmentation on the increase in the risk of species extinction



Source: Modified from Jump and Peñuelas (2005).

FIGURE 4.7: Reduction in the number of species recruited in a scrubland area subjected to experimental warming and drought



Note: Values are the means (\pm SD) of three plots per treatment in which eight squares of 400 cm² were sampled during the period 1999-2002. Statistical significance values refer to comparisons between treatments and the control by means of repeat measure ANOVA.

Source: Modified from Lloret, Peñuelas and Estiarte (2004).

Acknowledgments

There are many important examples of global change studies inspired by the ideas of Margalef and we cannot end this short chapter without recalling that our admired professor Margalef, as well as being a genius, was a good and kind man with the gift of simplicity; it is also these qualities that we are paying tribute to with this book. In concluding, we would like to repeat two pieces of advice from the many that he gave us, in case they may be of help to terrestrial ecologists in particular, and the scientific community in general. For the former, and without neglecting the molecular level, let us not forget to bang our heads against a tree from time to time, asking it for inspiration to help us understand the world. For the scientific community in general, we should consider nature from the viewpoint of a child: inquisitive, scrutinising and taking nothing for granted. We should question everything, not only to improve our research and our knowledge but because it is only when we play like children that we are really happy. Research should be a game, so let's go play! That is the greatest tribute we can give him.

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