

# THE WARMING-INDUCED EVOLUTION OF TERRESTRIAL PLANTS



CO<sub>2</sub>SCIENCE & SPPI ORIGINAL PAPER ♦ August 13, 2014

# THE WARMING-INDUCED EVOLUTION OF TERRESTRIAL PLANTS

**Citation:** Center for the Study of Carbon Dioxide and Global Change. "The Warming-Induced Evolution of Terrestrial Plants." Last modified August 13, 2014. [http://www.co2science.org/subject/e/summaries/evolution\\_natural.php](http://www.co2science.org/subject/e/summaries/evolution_natural.php).

One of the grandest of catastrophes that climate alarmists contend will result from CO<sub>2</sub>-induced global warming – which they predict will be unprecedented in terms of both the speed and level of warmth attained – is that many species of plants will not be able to migrate poleward in latitude or upward in altitude fast enough to remain within regions with temperature regimes suitable for their continued existence; and, therefore, they predict that many of them will likely be *driven to extinction*. But what if earth's plants can *evolve?* ... and evolve *fast enough* to shift their ranges at a rate commensurate with the rate at which temperatures may be warming? Or what if they can adjust their inner workings so as to be able to tolerate more heat than they seem to be capable of doing nowadays? These key questions are explored in detail in the papers that are briefly reviewed below.

[Gunter et al. \(2000\)](#)<sup>1</sup> introduced their study of the subject by noting that many models of actual or attempted range shifts in response to global warming lack a thorough understanding of "the role that acclimation and genetic adaptation may have in a species' response to predicted climate regimes," stating that if populations "have a greater capacity for adjustment to higher temperatures, and if they are not constrained by complete genetic isolation from other populations, then the effects of global warming will probably be less severe than what may be predicted from a simple temperature-response curve applied without regard to spatial or temporal genetic variation."

In exploring this possibility, the four researchers employed *random amplified polymorphic DNA* markers to evaluate population-level genetic structure as an indirect indicator of the capacity for response to environmental change by sugar maple trees from three geographical locations representing a north-south gradient of that species' current distribution. This work revealed, as they described it, that "genetic diversity, as indicated by estimates of percent polymorphic loci, expected heterozygosity, fixation coefficients, and genetic distance, is greatest in the southern region, which consists of populations with the maximum potential risk

*What if earth's plants  
can evolve? ... and evolve fast  
enough to shift their ranges  
at a rate commensurate with  
the rate at which  
temperatures may be  
warming?*



*Or what if they can adjust  
their inner workings so as to  
be able to tolerate more heat  
than they seem to be capable  
of doing nowadays?*

---

<sup>1</sup> <http://www.co2science.org/articles/V11/N37/EDIT.php>.

due to climate change effects," and that "the high degree of variation within sugar maple implies that it may contain genetic mechanisms for adaptation."

In discussing their findings, Gunter *et al.* noted that sugar maple range shift potentials derived by the Goddard Institute for Space Studies (Hansen *et al.*, 1983) and NASA's Geophysical Fluid Dynamics Laboratory (Manabe and Wetherald, 1987) - as described by Davis and Zabinski (1992) - "assume that a species grows only in a climate with temperature and precipitation identical to its current range." But in a significant rebuff of those studies and their alarmist implications, they went on to state that existing "high levels of genetic variation among families indicate that vegetational models designed to predict species' responses to global-scale environmental change may need to consider the degree and hierarchical structure of genetic variation when making large-scale inferences." And when the latter approach is taken, one finds that the ability of a species to adapt to a changing environment may be *far greater* than what is presumed by the outdated *climate envelope* approach.

Four years later, [Hamrick \(2004\)](#)<sup>2</sup> also noted there were concerns that (1) "expected changes may be of such an extent that tree species will not have adequate genetic variation to adapt to the modified conditions (Critchfield, 1984; Davis and Zabinski, 1992)," that (2) "environmental changes may occur at such a rapid rate that trees, with their long generation times, could not adapt quickly enough to keep pace with predicted changes (Davis and Shaw, 2001)," and that (3) trees "may not be capable of dispersing into newly available habitats quickly enough to match the rate of environmental change (Clark, 1998)."

In reviewing the findings of a number of studies that focused on the responses of trees to conditions analogous to those of computer-generated simulations of rapid global warming, however, Hamrick found that "trees combine life-history traits and levels of genetic diversity that will allow them to adapt relatively quickly to environmental changes," noting that they have high genetic mobility via pollen. The plant biology and genetics professor also noted that "tree species have faced large-scale global environmental changes many times during their evolutionary histories," and that even though these changes "occurred quite quickly, most tree species have survived," while maintaining traits that "may allow many tree species to survive predicted global climatic changes while preserving much of their genetic diversity."

In another intriguing paper, [Jump \*et al.\* \(2006\)](#)<sup>3</sup> introduced their study of potential tree responses to global warming by noting that "one of the basic assumptions in the study of plant adaptation to environment (genecology) is that natural selection in different environments generates genetic clines that correlate with environmental clines." Within this context, they further stated that "temperature is of major importance as a selective agent causing population differentiation over altitudinal and latitudinal clines (Saxe *et al.*, 2001)," and that "temporal changes in gene frequency that result from global warming should therefore mirror spatial changes observed with decreasing altitude and latitude," which changes are typically manifest in particular alleles that "may be confined to, or occur preferentially in, different sites with contrasting environmental conditions."

---

<sup>2</sup> <http://www.co2science.org/articles/V7/N45/B1.php>.

<sup>3</sup> <http://www.co2science.org/articles/V10/N5/EDIT.php>.

As a test of this hypothesis, the four researchers "combined population genomic and correlative approaches to identify adaptive genetic differentiation linked to temperature within a natural population of the tree species *Fagus sylvatica* L. [European beech] in the Montseny Mountains of Catalonia, northeastern Spain," concentrating on three areas: the upper treeline (high *Fagus* limit, HFL), the lower limit of *F. sylvatica* forest (low *Fagus* limit, LFL), and an area of the forest interior.

With respect to the temperature differential between the HFL and LFL locations, Jump *et al.* noted that the 648-meter altitudinal difference that separates them "equates to a mean temperature difference of 3°C ... based on the altitudinal lapse rate of 0.51°C per 100 meters reported by Penuelas and Boada (2003) for Montseny." Likewise, with respect to the change in temperature due to the region's manifestation of 20th-century global warming, they said that "by 2003, temperatures had increased by approximately 1.65°C when compared with the 1952-1975 mean," which temperature change, as they saw it, was "likely to represent a strong selection pressure."

Numerous tests conducted by Jump *et al.* on the data they collected revealed that the frequency of a particular *F. sylvatica* allele showed a predictable response to both altitudinal and temporal variations in temperature, with a declining frequency and probability of presence at the HFL site that the Spanish research team determined to be "in parallel with rising temperatures in the region over the last half-century." And as a result, they stated that their work "demonstrates that adaptive climatic differentiation occurs between individuals within populations, not just between populations throughout a species geographic range," which further suggests, in their words, that "some genotypes in a population may be 'pre-adapted' to warmer temperatures (Davis and Shaw, 2001)."

Jump *et al.* also went on to contend that "the increase in frequency of these genotypes," which occurred in their study in parallel with rising temperatures, "shows that current climatic changes are now imposing directional selection pressure on the population," and that "the change in allele frequency that has occurred in response to this selection pressure also demonstrates that a significant evolutionary response can occur on the same timescale as current changes in climate," additionally citing in this regard the studies of Davis *et al.* (2005), Jump and Penuelas (2005) and Thomas (2005).

In concluding, Jump *et al.* thus suggested that an evolutionary response to global warming of the type they described is likely already "underway," which further suggests that many species of plants likely will *not* be forced to migrate either poleward in latitude or upward in altitude in response to global warming, as climate alarmists adamantly claim they will be forced to do. Instead, they will have the *opportunity* to so adjust their ranges (i.e., *expand* them) at the *cold*-limited boundaries of their ranges, but they may not be forced to make any major changes at the *heat*-limited boundaries of their ranges, due in part to the phenomenon elucidated by Jump *et al.*

Jumping ahead five years, [Keller et al. \(2011\)](http://www.co2science.org/articles/V14/N21/C2.php)<sup>4</sup> introduced their work by noting that "studies on the evolution of plant populations during historical fluctuations in climate can reveal the capacity for and constraints on adaptive evolution and may help inform predictions about evolutionary responses to future environments." And thus imbued with this optimism, they tested for adaptive variation in thirteen ecophysiology and phenology traits on clonally propagated genotypes of balsam poplar (*Populus balsamifera* L.) trees originating from a range-wide sample of 20 sub-populations that developed during the warming of climate conditions that marked the end of the last glacial maximum (~18 thousand years ago), when there was a rapid environmental change that increased population sizes and led to range expansions in many plant species, which "wave of migrations," in their words, "affected genomic diversity within populations, as colonists sub-sampled alleles from the ancestral gene pool during the process of expansion," as described by Lascoux *et al.* (2004), Petit *et al.* (2004) and Savolainen and Pyhajarvi (2007). And when all was said and done, the six scientists reported that "evidence for divergence in excess of neutral expectations was present for eight of thirteen traits," while noting that "strong correlations were present between traits, geography [extending across the whole of Canada from the Atlantic to Pacific Oceans], and climate," revealing "a general pattern of northern subpopulations adapted to shorter, drier growing seasons compared with populations in the center or eastern regions of the range."

As for the implications of these findings, Keller *et al.* affirmed that their study "demonstrates pronounced adaptive variation in ecophysiology and phenology among balsam poplar populations." And they further stated that this result suggests that "as this widespread forest tree species expanded its range since the end of the last glacial maximum, it evolved rapidly in response to geographically variable selection." Therefore, it can be expected to do so again, as circumstances may warrant; for as they remarked in the concluding sentence of their paper, "balsam poplar is both highly variable and capable of a broad range of adaptive physiological responses to a changing climate."

In introducing their huge collaborative study one year later, [Niu et al. \(2012\)](http://www.co2science.org/articles/V15/N38/B2.php)<sup>5</sup> wrote that "it is well documented that plants (Mooney *et al.*, 1978; Berry and Bjorkman, 1980; Atkin and Tjoelker, 2003), animals (Parmesan, 2006), and microbes (Bradford *et al.*, 2008) acclimate and/or adapt to prevailing environmental conditions in a way that can optimize their functioning under varying temperatures, which is collectively termed optimality (Parker and Maynard Smith, 1990)," and they hypothesized that "the integrated response of an ecosystem, as an assemblage of interacting organisms, might also demonstrate thermal optimality under temperature change," citing Loreau (2010).

In a study designed to test the merits of their hypothesis, Niu *et al.* "compiled data from 169 globally distributed sites of eddy covariance and quantified the temperature response functions of net ecosystem exchange (NEE), an ecosystem-level property, to determine whether NEE shows thermal optimality and to explore the underlying mechanisms."

---

<sup>4</sup> <http://www.co2science.org/articles/V14/N21/C2.php>.

<sup>5</sup> <http://www.co2science.org/articles/V15/N38/B2.php>.

In discussing their findings, the international team of 68 researchers - hailing from Australia, Austria, Belgium, Canada, China, the Czech Republic, Denmark, Finland, France, Germany, Ireland, Italy, Japan, the Netherlands, Russia, Sweden, Switzerland, the United Kingdom and the United States - said they found that "the temperature response of NEE followed a peak curve, with the optimum temperature (corresponding to the maximum magnitude of NEE) being positively correlated with annual mean temperature over years and across sites." And they stated that "shifts of the optimum temperature of NEE were mostly a result of temperature acclimation of gross primary productivity (upward shift of optimum temperature) rather than changes in the temperature sensitivity of ecosystem respiration." In addition, they indicated that "extended growing seasons, increased nitrogen mineralization, and enhanced root growth (Penuelas and Filella, 2001; Churkina *et al.*, 2005; Luo *et al.*, 2009) may also have contributed to the increased CO<sub>2</sub> uptake under higher temperatures, leading to the upward shift in the optimum temperature of gross primary productivity in warmer years." Be that as it may, if the world begins to warm again, for *whatever* reason, we can probably expect the bulk of the planet's vast array of ecosystems to become even *more* productive than they are today.

In a concurrent study that came to much the same conclusion, [Pluess and Weber \(2012\)](#)<sup>6</sup> wrote that "with increasing temperatures and dryer summers [as predicted by various climate models], areas nowadays covered by beech forests are expected to shrink tremendously," but they added that "if individuals at the dry distribution limits [of the species: *Fagus sylvatica* L.] are adapted to lower moisture availability, *F. sylvatica* might contain the genetic variation for the continuation of beech forests under climate change," even in areas that are predicted to become devoid of the trees.

In an investigation into the strength of this hypothesis, the two researchers used an AFLP (Amplified Fragment Length Polymorphism) genome scan approach that was designed to explore the "neutral and potentially adaptive genetic variation in *Fagus sylvatica* in three regions [within the lowland forests of Switzerland] containing a dry and mesic site each," after which they "linked this dataset with dendrochronological growth measures and local moisture availabilities based on precipitation and soil characteristics." This approach to the issue indicated that a "potential for adaptation to water availability" was reflected in observed outlier alleles that "indicated micro-evolutionary changes between mesic and dry stands." They also noted, in this regard, that "while Rose *et al.* (2009) found adaptation to drought in a common garden experiment with seedlings originating from provenances which were more than 1000 km apart," they found genetic differentiation in relation to water availability in *neighboring* stands. And in light of this set of real-world observations, Pluess and Weber concluded that "dispersal across large distances is thereby not

*If the world begins to warm again, for whatever reason, we can probably expect the bulk of the planet's vast array of ecosystems to become even more productive than they are today.*

---

<sup>6</sup> <http://www.co2science.org/articles/V15/N43/B1.php>.

needed for the spread of 'pre-adapted' genes in *F. sylvatica*," for the trees apparently do indeed contain the genetic material needed for "the continuation of beech forests under climate change," even in areas that have been predicted to become too dry for *F. sylvatica* trees to survive.

Contemporaneously, [Hahn et al. \(2012\)](http://www.co2science.org/articles/V16/N8/B1.php)<sup>7</sup> noted that "altitudinal gradients comprise an assemblage of environmental, especially climatic, variables which influence the distribution of plant species and, potentially, population genetic variation," while stating that it has consequently been concluded by some that climate change may alter species distributions with the result that, locally, certain species "might become extinct," citing in this regard Sala *et al.* (2000) and Thomas *et al.* (2004). The basis for this ominous conclusion, as the six scientists described it, derives from the fact that "habitat suitability typically decreases at the upper edge of the altitudinal range where population size might decline," plus the observation that "in small populations genetic diversity is often reduced and inbreeding may increase (Lynch *et al.*, 1995; Young *et al.*, 1996)," with the result that "low genetic diversity and high inbreeding potentially cause loss of fitness due to fixation of deleterious alleles and inbreeding depression (Ouborg *et al.*, 1991; Lynch *et al.*, 1995; Young *et al.*, 2002), which could affect future population persistence."

Nevertheless, and questioning the generality of this suite of speculations, Hahn *et al.* investigated patterns of population genetic variation in three common plants of semi-dry grasslands - *Briza media*, a wind-pollinated grass, and *Trifolium montanum* and *Ranunculus bulbosus*, both of which are insect-pollinated herbs - at upper peripheral and lower more central altitudes in the Swiss Alps using the *amplified fragment length polymorphism* (AFLP) technique. And what did they learn?

The Swiss researchers determined that contrary to what many had long supposed, altitude had *not* affected genetic diversity in the grassland species they studied. In fact, they reported that their study indicated that "populations at the upper periphery are not genetically depauperate or isolated," and that they thus may be "important populations for migration under climate change." So thus it was that Hahn *et al.* concluded that what they called the "potentially pre-adapted genes" of the three plant species they studied might well "spread easily across altitudes," which would help to *prevent* their local extinction in a potentially warming world of the future.

More recently, [Thompson et al. \(2013\)](http://www.co2science.org/articles/V16/N34/B2.php)<sup>8</sup> stated that "in addition to changes in distribution and plasticity, an evolutionary response to climate change may occur if species evolve a genetically-based adaptation to climate change," citing Chevin *et al.* (2010) and Hoffmann and Sgro (2011), while noting that "it is important to distinguish this genetic response from a plastic response of individuals if we are to fully understand the evolutionary potential of species to evolve with climate change," as has been described by Gienapp *et al.* (2008). And, therefore, to test the hypothesis that phenolic chemotypes (thymol and carvacrol) of Mediterranean wild thyme (*Thymus vulgaris*) now occur in sites where they were previously absent or have increased their

---

<sup>7</sup> <http://www.co2science.org/articles/V16/N8/B1.php>.

<sup>8</sup> <http://www.co2science.org/articles/V16/N34/B2.php>.

frequency in transitional sites due to a relaxation of selection normally associated with extreme early-winter freezing, the team of eight researchers compared the chemotype composition of populations observed in the early 1970s (Vernet *et al.*, 1977) to that found in 2009-2010 for 36 populations sampled along six transects in and around the Saint Martin-de-Londres basin, which covers an area of about 80 km<sup>2</sup> with southern limits about 20 km north of Montpellier in the Mediterranean climate region of southern France.

As a result of these efforts, the eight French researchers discovered "a rapid and probably ongoing spatial reorganization of a genetic polymorphism that is closely associated with a warming of extreme winter freezing events on a highly localized spatial scale," observing "both a significant appearance of freezing-sensitive phenolic chemotypes in sites where they were historically absent and an increase in their frequency in previously mixed populations." And in light of these findings, Thompson *et al.* concluded that their study, "done over a similar time span as work reporting ecological changes in plant species distribution, illustrates that a rapid evolutionary response to temperature modifications can occur where genetic variation is combined with a change in a previously strong selection pressure, even for a perennial woody plant."

Last of all, [Matter \*et al.\* \(2013\)](http://www.co2science.org/articles/V16/N41/B2.php)<sup>9</sup> introduced their contribution to the subject by writing that "gene flow connects populations, maintains genetic diversity, prevents inbreeding and facilitates the spread of adaptive genes across a species range," citing Slatkin (1985, 1987) and Ellstrand and Elam (1993), while further stating that "understanding how plant populations are connected by gene flow, particularly across altitudinal gradients in mountain regions, will improve our understanding of how they will respond to future environmental change." And in an attempt to gain some of that important "understanding," the four Swiss scientists studied patterns of historic gene flow, flowering phenology and contemporary pollen flow in two common herbs (*Ranunculus bulbosus* and *Trifolium montanum*) along an altitudinal gradient of 1200-1800 meters a.s.l. over a distance of 1 km among five alpine meadows in Switzerland.

This work revealed, as they described it, that "historic gene flow was extensive," with their data suggesting that "contemporary pollen flow is not limited across altitudes in either species." And so they concluded that "high levels of pollen flow among altitudes in both *R. bulbosus* and *T. montanum* should facilitate exchange of genes which may enhance adaptive responses to rapid climate change."

*Considered in their entirety,  
the observations discussed  
suggest that earth's plants  
may be much better prepared  
to meet whatever climatic  
challenges the future may pose  
for them than what almost  
everyone had once believed.*

---

<sup>9</sup> <http://www.co2science.org/articles/V16/N41/B2.php>.



In conclusion, and considered in their entirety, the observations discussed above suggest that earth's plants may be much better prepared to meet whatever climatic challenges the future may pose for them than what almost everyone had once believed.

## References

Atkin, O.K. and Tjoelker, M.G. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science* **8**: 343-351.

Berry, J. and Bjorkman, O. 1980. Photosynthetic response and adaptation to temperature in higher-plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **31**: 491-543.

Bradford, M.A., Davies, C.A., Frey, S.D., Maddox, T.R., Melillo, J.M., Mohan, J.E., Reynolds, J.F., Treseder, K.K. and Wallenstein, M.D. 2008. Thermal adaptation of soil microbial respiration to elevated temperature. *Ecology Letters* **11**: 1316-1327.

Chevin, L.-M., Lande, R. and Mace, G.M. 2010. Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLoS Biology* **8**: 10.1371/journal.pbio.1000357.

Churkina, G., Schimel, D., Braswell, B.H. and Xiao, X.M. 2005. Spatial analysis of growing season length control over net ecosystem exchange. *Global Change Biology* **11**: 1777-1787.

Clark, J.S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and the paleorecord. *American Naturalist* **152**: 204-224.

Critchfield, W.B. 1984. Impact of the Pleistocene on the genetic structure of North American conifers. In: Tanner, R.M. (Ed.), *Proceedings of the Eighth North American Forest Biology Workshop*. Logan, Utah, USA, pp. 70-118.

Davis, M.B. and Shaw, R.G. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* **292**: 673-679.

Davis, M.B., Shaw, R.G. and Etterson, J.R. 2005. Evolutionary responses to changing climate. *Ecology* **86**: 1704-1714.

Davis, M.B. and Zabinski, C. 1992. Changes in geographical range resulting from greenhouse warming: Effects on biodiversity of forests. In: *Global Warming and Biological Diversity*, Peters, R.L. (Ed.), Yale University Press, New Haven, Connecticut, USA, pp. 297-308.

Ellstrand, N.C. and Elam, D.R. 1993. Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology and Systematics* **24**: 217-242.

Gienapp, P., Teplitsky, C., Alho, J.S., Mills, J.A. and Merila, J. 2008. Climate change and evolution: Disentangling environmental and genetic responses. *Molecular Ecology* **17**: 167-178.

- Gunter, L.E., Tuskan, G.A., Gunderson, C.A. and Norby, R.J. 2000. Genetic variation and spatial structure in sugar maple (*Acer saccharum* Marsh.) and implications for predicted global-scale environmental change. *Global Change Biology* **6**: 335-344.
- Hahn, T., Kettle, C.J., Ghazoul, J., Frei, E.R., Matter, P. and Pluess, A.R. 2012. Patterns of genetic variation across altitude in three plant species of semi-dry grasslands. *PLoS ONE* **7**: e41608.
- Hamrick, J.L. 2004. Response of forest trees to global environmental changes. *Forest Ecology and Management* **197**: 323-335.
- Hansen, J., Russell, G., Rind, D., Stone, P., Lacis, A., Lebedeff, S., Ruedy, R. and Travis, L. 1983. Efficient three-dimensional global models for climate studies: Models I and II. *Monthly Weather Review* **111**: 609-662.
- Hoffmann, A.A. and Sgro, C.M. 2011. Climate change and evolutionary adaptation. *Nature* **470**: 479-485.
- Jump, A.S., Hunt, J.M., Martinez-Izquierdo, J.A. and Penuelas, J. 2006. Natural selection and climate change: temperature-linked spatial and temporal trends in gene frequency in *Fagus sylvatica*. *Molecular Ecology* **15**: 3469-3480.
- Jump, A.S. and Penuelas, J. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters* **8**: 1010-1020.
- Keller, S.R., Soolanayakanahally, R.Y., Guy, R.D., Silim, S.N., Olson, M.S. and Tiffin, P. 2011. Climate-driven local adaptation of ecophysiology and phenology in balsam poplar, *Populus balsamifera* L. (Salicaceae). *American Journal of Botany* **98**: 99-108.
- Lascoux, M., Palme, A.E., Cheddadi, R. and Latta, R.G. 2004. Impact of ice ages on the genetic structure of trees and shrubs. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* **359**: 197-207.
- Loreau, M. 2010. Evolution of ecosystems and ecosystem properties. In: Loreau, M. (Ed.). *From Populations to Ecosystems, Theoretical Foundations for a New Ecological Synthesis*. Princeton University Press, Princeton, New Jersey, USA, p. 225-259.
- Luo, Y., Sherry, R., Zhou, X. and Wan, S. 2009. Terrestrial carbon-cycle feedback to climate warming: experimental evidence on plant regulation and impacts of biofuel feedstock harvest. *Global Change Biology Bioenergy* **1**: 62-74.
- Lynch, M., Conery, J. and Burger, R. 1995. Mutation accumulation and the extinction of small populations. *The American Naturalist* **146**: 489-518.
- Manabe, S. and Wetherald, R.T. 1987. Large-scale changes in soil wetness induced by an increase in carbon dioxide. *Journal of Atmospheric Sciences* **44**: 1211-1235.

Matter, P., Kettle, C.J., Ghazoul, J. and Pluess, A.R. 2013. Extensive contemporary pollen-mediated gene flow in two herb species, *Ranunculus bulbosus* and *Trifolium montanum*, along an altitudinal gradient in a meadow landscape. *Annals of Botany* **111**: 611-621.

Mooney, H.A., Bjorkman, O. and Collatz, G.J. 1978. Photosynthetic acclimation to temperature in desert shrub, *Larrea-divaricata*. 1. Carbon-dioxide exchange characteristics of intact leaves. *Plant Physiology* **61**: 406-410.

Niu, S., Luo, Y., Fei, S., Yuan, W., Schimel, D., Law, B.E., Ammann, C., Arain, M.A., Arneth, A., Aubinet, M., Barr, A., Beringer, J., Bernhofer, C., Black, T.A., Buchmann, N., Cescatti, A., Chen, J., Davis, K.J., Dellwik, E., Desai, A.R., Etzold, S., Francois, L., Gianelle, D., Gielen, B., Goldstein, A., Groenendijk, M., Gu, L., Hanan, N., Helfter, C., Hirano, T., Hollinger, D.Y., Jones, M.B., Kiely, G., Kolb, T.E., Kutsch, W.L., Lafleur, P., Lawrence, D.M., Li, L., Lindroth, A., Litvak, M., Loustau, D., Lund, M., Marek, M., Martin, T.A., Matteucci, G., Migliavacca, M., Montagnani, L., Moors, E., Munger, J.W., Noormets, A., Oechel, W., Olejnik, J., Paw U., K.T., Pilegaard, K., Rambal, S., Raschi, A., Scott, R.L., Seufert, G., Spano, D., Stoy, P., Sutton, M.A., Varlagin, A., Vesala, T., Weng, E., Wohlfahrt, G., Yang, B., Zhang, Z. and Zhou, X. 2012. Thermal optimality of net ecosystem exchange of carbon dioxide and underlying mechanisms. *New Phytologist* **194**: 775-783.

Ouborg, N.J., Treuren, R. and Damme, J.M.M. 1991. The significance of genetic erosion in the process of extinction. *Oecologia* **86**: 359-367.

Parker, G.A. and Maynard Smith, J. 1990. Optimality theory in evolutionary biology. *Nature* **348**: 27-33.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution and Systematics* **37**: 637-669.

Penuelas, J. and Boada, M. 2003. A global change-induced biome shift in the Montseny Mountains (NE Spain). *Global Change Biology* **9**: 131-140.

Penuelas, J. and Filella, I. 2001. Phenology - Responses to a warming world. *Science* **294**: 793-795.

Petit, R.J., Bialozyt, R., Garnier-Gere, P. and Hampe, A. 2004. Ecology and genetics of tree invasions: From recent introductions to Quaternary migrations. *Forest Ecology and Management* **197**: 117-137.

Pluess, A.R. and Weber, P. 2012. Drought-adaptation potential in *Fagus sylvatica*: Linking moisture availability with genetic diversity and dendrochronology. *PLoS ONE* **7**: 10.1371/journal.pone.0033636.

Rose, L., Leuschner, C., Kockemann, B. and Buschmann, H. 2009. Are marginal beech (*Fagus sylvatica* L.) provenances a source for drought tolerant ecotypes? *European Journal of Forest Research* **128**: 335-343.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M. and Wall, D.H. 2000. Global biodiversity scenarios for the year 2100. *Science* **287**: 1770-1774.

Savolainen, O. and Pyhajarvi, T. 2007. Genomic diversity in forest trees. *Current Opinion in Plant Biology* **10**: 162-167.

Saxe, H., Cannell, M.G.R., Johnsen, B., Ryan, M.G. and Vourlitis, G. 2001. Tree and forest functioning in response to global warming. *New Phytologist* **149**: 369-399.

Slatkin, M. 1985. Gene flow in natural populations. *Annual Review of Ecology and Systematics* **16**: 393-430.

Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. *Science* **236**: 787-792.

Thomas, C.D. 2005. Recent evolutionary effects of climate change. In: Lovejoy, T.E. and Hannah, L. (Eds.), *Climate Change and Biodiversity*, Yale University Press, New Haven, Connecticut, USA, pp. 75-88.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Barend, F., Erasmus, N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. and Williams, S.E. 2004. Extinction risk from climate change. *Nature* **427**: 145-148.

Thompson, J., Charpentier, A., Bouguet, G., Charmasson, F., Roset, S. Buatois, B., Vernet, P. and Gouyon, P.-H. 2013. Evolution of a genetic polymorphism with climate change in a Mediterranean landscape. *Proceedings of the National Academy of Sciences* **110**: 2893-2897.

Vernet, P, Guillerm, J.L. and Gouyon, P.H. 1977. Le polymorphisme chimique de *Thymus vulgaris* L. (Labiée) I. Repartition des formes chimiques en relation avec certains facteurs écologiques. *Oecologia Plantarum* **12**: 159-179.

Young, A.G., Boyle, T.J.B. and Brown, A.H.D. 1996. The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology and Evolution* **11**: 413-418.

Young, A.G., Hill, J.H., Murray, B.G. and Peakall, R. 2002. Breeding system, genetic diversity and clonal structure in the sub-alpine forb *Rutidosis leiolepis* F. Muell. (Asteraceae). *Biological Conservation* **106**: 71-78.



*Cover photo taken by Bret Stewart in the Big Horn Mountains, Wyoming, USA.*

