**FOREST GENETIC TOOLS TO IMPROVE FOREST RESILIENCE TO CLIMATE CHANGE AND FOREST HEALTH**

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Abstract:

Forest health parameters respond to climate change having a direct impact on forest resilience. Intensification of human impact on ecosystem within the last decades has led to unexpected disturbances in the resilience of forest ecosystem on a global level as well as the provisions made for ecosystem services. The current Anthropocene era has led us to reconsider the forest management approach and to device new management practices having flexible nature and better dealing with global climate changes. This review aims to focus on the contemporary forest genetic tools, their utility and limitations with respect to improvement of forest resilience, climate change and forest health. Potential implications of genetic tools in forest management, its goals and principles and its response reveal the role of genetically diverse and adapted seeds and stock to be the foundation of forest health and ecosystem in addition to major contribution of gene conservation in vulnerable species and population preservation for future generations. Adaptive implementation owing to climate change require new tools, methodologies, skilled workforce, better infrastructure, re – focused investments as well as refined and reliable research and management.

**Keywords: Forest Resilience, Forest Health, Climate change, Genetic tools, gene conservation.**

**INTRODUCTION**

Forest health has been the prime concern of forest pathologists including the symptom and causes as well as preventive measures to maintain forest health. There has been a shift in perspective pertaining to forest health towards tree disease and their important role in forest ecosystem mechanisms as well as the ecological health (Franklin et al., (1987), Teale and Castello, 2011). In lieu of this, it can be observed that the effect of native fungal diseases has been evident in maintenance of diversity in the forest as they facilitate the species to be more resilient towards other types of disturbances (Hansen 1999, Hansen and Goheen 2000). Exotic trees have high biodiversity and aesthetics but low commercial value due to their controlled and uniform plantation owing to native and exotic tree diseases, maintaining a controlled biodiversity (Carnuset al.,2006), Lombardero et al., 2012). On the contrary, the whole ecosystem can be threatened as a result of some tree species extinction owing to the act of some invasive exotic pathogens (Roberge et al., 2011, Cobb et al., 2013, Cahill et al., 2008, Davis et al., 2014).

**FOREST HEALTH RISKS**

Major contributors in forest change are lack of management, over exploitation, degradation, habitat fragmentation, species distribution shifts and ecological succession. In addition, there has been also a shift in forest development from traditionally sustainable timber production to its multipurpose role in recreation and as a source of clean air and water (MacDonald, 2003, Hepting and Cowling 1977, Petrokofsky et al., 2010). Along with that an increase in the trade of plant commodities to remote and faraway places globally and the effect of change in climate has further impacted retrogressively on the condition of forest health (Wingfield, 1990, Holdenrieder, 2000). Excessive trade and climate change can lead to greater risks of establishment, spread and influence of newer and dangerous pests and pathogens. Lack of taxonomical morphologic expertise recently due to retirement without replacement along with rapid updation of new molecular methodological advances are one of the major concerns in forest ecosystem disturbances (Gadoury et al., 2009, MacDonald et al., 2009, Hamelin, 2012, Wood and Gebhardt, 2013). Regional outbreak of exotic tree fungal pathogens can be better understood using landscape ecology tools and forest pathology perspectives (Holdenrieder et al., 2004, Hatala et al., 2011). Diversity studies of endophytes of tree species provide insights of tree health (Sieber, 2007, Witzell et al., 2014) in addition to implementation of conservational biology tools pertaining to tree disease (Orwig 2002; Holzmueller et al., 2010; Pautasso et al., 2013 ;Shearer et al., 2013). In this rapidly evolving ecological aspect, the major aim of the present study lies in the selective evaluation of forest health, climate change and its effects on forest resilience. Secondarily, this study attempts to map out bridges between forest health, climate change and forest resilience with other aspects. Keeping in mind the time and space constrains, the focus has been mainly concentrated on the different genetical tools used in these three regions and their overall effect.

Human forced global climate change superimposed many different anthropogenic impacts on forest ecosystem. Rate of photosynthesis and respiration are readily influenced by climate change (Friberg et al., 2011, Jiao et al 2015, Kueppers et al., 2004). Other factors include forest temperature, radiation, and moisture in addition to medium and long climate periods. Short term process like frequency of storm and wild fires, herbivory and species migration are also influenced by climate and weather conditions. Biophysical forest process rate along with species’ physiological tolerance are altered causing change in forest ecosystem owing to global climate changes (Olesen et al., 2007, Kellomaki et al., 2008, Malhi et al., 2008).

Forest is a self-organised and complex system which is equipped with multiple natural occurrences responding to the intrinsic and extrinsic factors. As in the height and density of tree canopy are dependent on the water availability revealing the echo physiological relationship between environmental controls and plant growth (Berry and Roderick, 2002). There will be evident change in the forest ecosystem and species composition in response to climate change and specifically reduction in water availability. Upon reaching a threshold the vegetation beyond this limit will be lacking the characteristic taxonomic composition like in extreme arid conditions forest may reduce to savannas or grasslands while in case of rainforest, the high temperature may show closed boreal canopy having sufficient moisture for an extended growing season (Price and Scott, 2006; Kellomaki et al., 2008).

Regional climates are also affected by the availability of forest as evident from the Amazon forests (Betts et al., 2008; Phillips et al., 2009). Large number of literatures is available with respect to climate change and forests (Bonan et al., 2003; Callaghan et al., 2004). Climatic changes like moisture change (Bonan et al., 2003), energy fluxes (Wilson and Agnew, 1992), forest fire and herbivory (Ayres and Lomardero, 2000), carbon cycle systems (Phillips et al., 2009) emphasize the importance of maintaining forest resilience in order to cope up with the climatic changes and to survive under such conditions.

Forest resilience or the ability of the ecosystem to regain its original state after perturbation and the maintenance of its characteristic composition, structure, function, and process rates (Holling, 1973). In other words, ability of the forest system to tackle with the disturbance and not being affected, retaining its own basic structure and function, is termed as forest resilience (Walker and Salt, 2012). Forest give different responses to different types of disturbances and climatic changes, and depending upon its capability to cope up, the forest may show variation in its characteristic taxonomy and ecological processes and may also be altered in certain conditions. The state of a forest ecosystem represents its most dominant species assemblage at that location in the ecosystem, their functional roles, characteristic morphology and features like height, layers etc. and these define the state of forest in a mature forest type. Many researchers have worked and differentiated engineering resilience and ecological resilience (Holling, 1973; Peterson et al., 1998; Gunderson, 2000; Walker et al., 2004). The former refers to the ability of the ecosystem to return to its exact state after a disturbance. It is characterised by only one steady state and is also known as equilibrium dynamics. On the contrary, ecological resilience is the ability to face the disturbance and bear with the adverse conditions before reaching a threshold after which the forest ecosystem changes completely to another state and is also known as the non-equilibrium dynamics.

Resilience is eminent property of ecosystem being conferred at different levels like genes, species, functional groups, and processes (Gunderson 2000; Drever et al., 2006) and is maintained as an important characteristic feature owing to societal adaptation to climate change as suggested by various researchers (Millar et al., 2007; Chapin et al., 2010). Forest shows the property of resistance towards little changes within bounds owing to non-catastrophic variations like chronic and dynamic insect herbivory, minor blowdown, or canopy gaps due to tree deaths individually or in groups. Forests are also resistant to environmental changes like weather patterns due to redundancy at functional species level. There has been evidence of high resilience in the ecosystem, but low resistance towards perturbation. However, contrary situation is seen in well-developed forests, especially primary forests, having both the properties of resilience and resistance towards changes (Drever et al., 2006). Resistance denotes stability, showing the capability of ecosystem to maintain a dynamic equilibrium by absorbing disturbances and being constant over longer periods of time.

**ISSUES OF SCALE AND RESILIENCE.**

A theoretical method is dependent on its proper scaling. Majority of the studies based on resilience focus on the reason behind change or maintenance of a particular state, while scaling studies focus on the evaluation of phenomena responsible for steady state ecosystems (Holling, 1973). Species level beta diversity enhances ecosystem resilience to adapt for the large-scale climate change through redundancy level of regional species pool. Resilience needs a temporal component related to disturbance, frequency, and ecosystem recovery, which is considered over many decades to centuries (Thompson et al., 2009). The change in ecosystem is caused due to environmental change or disturbance which is having a high magnitude.

**GENETIC DIVERSITY AND RESILIENCE TO CLIMATE CHANGE.**

As resilience attributes different levels in the biodiversity, the genetic species composition becomes the most fundamental feature. Molecular variation among species within forest community, within ecosystem diversity, across a geographical area shows biological diversity. This genotypic variation among population is the basic expression of biological diversity. Individuals at population level contributing to each level of ecological hierarchy undergo natural selection adding to resilience of species and forest ecosystem (Muller-Starck et al., 2005). Diversity fosters natural regeneration and help in adaptation towards climatic changes occurring in the quaternary period and needs to be maintained in order to face the challenges posed by anthropogenic global warming. Genetic variation forms the basis of natural selection of genotypes within species in response to environmental fluctuations (Etterson 2004; Reusch et al., 2005; Schaberg et al., 2008). This largely depends on the in situ genetic variation among each population of species (Bradshaw 1991).

Exposure to environmental changes decides the rate of adaptation of that population, its dispersal, or its fate otherwise (Burger and Lynch 1995). Range of fundamental eco physiological tolerance of a species is the expression of its genetic diversity range. Interspecific competitive interactions, in addition to dispersal method, are the primary determinants of response to change in a particular species (Halpin, 1997). In addition to adaptation, migration also plays role in responding towards evident climatic change. Many researchers have suggested diversification as a best tool to adaptation towards unpredictable climatic conditions (Ledig and Kitzmiller 1992, Millar et al., 2007). The two main means of adaptation towards change as shown by a particular species, include the dispersal of seed or vegetative propagules towards favourable environmental condition for survival or through change in their gene frequency to encourage genotypes capable of adaptation to the climatic variation (Burdon and Thrall 2001; Reusch et al., 2005). Another method of adaptation includes phenotypic plasticity, if permitted by the genotype (Nussey et al., 2005). Gene flow is further enhanced by dispersal among fragmented trees species, resulting in maintenance of genetic diversity. Prevention of genetic drift and loss of genetic diversity caused due to inbreeding within small isolated community of tree species (Fuchs and Hamrick, 2010; Farwig et al., 2008).

In general, genetic diversity of a forest ecosystem is maintained through seed and pollen dispersal, affecting the silence over change in the long term with respect to space and time in addition to re-establishment on favourable grounds. However, this capacity may have been reduced owing to anthropogenic intervention in landscape and gene pool. Genetic and reproductive activity of populations is potentially affected by population fragmentation. This generates a concern regarding the idea of in situ resilience owing to potential genetic adaptation, there are both short and long term components with respect to adaptation at genetic level, which enables variability in gene frequencies promoting growth and reproduction in an altered environment. Higher degree of diversity within natural populations is responsible for population stability in different environments (Namkoong et al., 1996), potential pollutants (Kull et al., 2007; Cantin et al., 2020) and pest species (Thrall et al., 2001). These concerns exaggerate the need for genetically diverse species to overcome the predicted climate change (IPCC 2007), which is too quick for a species to be able to prepare itself for adaptation over the low diversity level species in the forest population.

Forests are generally undomesticated and exhibit a very high level of genetic diversity owing to effective population size, local adaptation, and neutrality in the evolution process among heterogeneous environment (Hamrick 1986). Operational programmes of tree reading and related infrastructure like seed and seedling production are active since mid-1900’s. Forest biologists have used proven trials for seed selection of important commercial species over in the last 200 years and to assess the seed distance without compromising local adaptation under suitable climate (Aitken and Bemmels 2015, Langlet 1971). Molecular biology techniques are being utilised in this area since 1990’s and early 2000s. Techniques like QTL mappings have facilitated the marker aided selection of growth, productivity, and other wood qualities. Since then, highly polygenic nature of economically and environmentally important traits have been evident (Manolio et al., 2009). Due to drop in cost of sequencing, the focus of forest genetics research has moved towards the search related to single genes with great impact in addition to testing small target set of genes in place of genome wide scan, in order to tackle the contemporary demand of climate change, forest health, adaptation, resistance and commercial issues pertaining to biotic and abiotic stress.

Forest genomics in insects and disease resistance and early detection.

Moving from economic trades like growth and wood quality are now replaced by pest resistance genes owing to non-native insects and disease impact in addition to some natives species of pest with increased range and impact pertaining to climate change. Genomic tools help to

a. Understanding genomic architecture of insects and disease resistance or tolerance. b. To Select tree species which can survive/ thrive under the presence of these pests.

c. To detect the invasive species of pests and pathogens.

This can be better understood by American chestnut example (Castanea dentata) (Westbrook et al., 2019). Chestnut blight fungus (Cryphonectria paresilica) in USA is a threat to American chestnut tree population. To overcome this problem, the American Chestnut Foundation, TACF has started a breeding programme between blight resistant Chinese chestnut (Castanea mollissima) and American chestnut (Castanea dentata). Only a few major loci bear blight resistance and thus between (blight resistant Chinese chestnut) Castanea mollissima X Castanea dentata (American chestnut) (F1 generation) upon backcross over 3 generations and then inter-crossed to Castanea dentata (American chestnut) progeny resulted in large production of BC3F2 trees between 2000 to 2018. Among these BC3F2 trees, about 1/3 were identified as potential parents for further generations (Westbrook et al. 2019) have developed genomic prediction models for blight resistance and have found it accurate as compared to pedigree analysis which makes it cost and time effective all alone. They also revealed blight resistance as well as the trade-off between the two species followed polygenic inheritance. TACF considered different options in development of resistant trees, namely inclusion of different chestnut sources of resistance via marker-assisted introgressive system and secondly the technique to establish transgenic method to be used to develop resistant Castanea dentata (New House et al., 2014).

Distribution and abundance of insect pests are equivocal to climate change, making it a serious factor. As evident in case of mountain pine beetle (MPB: Dendroctonus ponerosae) apparent in western North America. Warmer winter temperatures have caused its increased population exponentially (Safranyik et al., 2010). MBP has resulted in substantial mortality in Lodgepool pine (Pinus contorta) and Jack pine (Pinus banksiana) in Western Canada. Being one of the dominant parts of the forest ecosystem, these have caused profound ecological and economic complications, leading to demand of MPB resistant species to be breed in order to restore the areas. Cullingham et al., (2019) identified two important loci related to resistance using transcriptional profiling and selection tests. One of these two loci show consistent association with resistance in case of Lodgepool pine (Pinus contorta). This may facilitate in the development of genome wide marker-aided selection or genomic selection tools in breeding programmes.

**ADAPTATION TO CHANGING CLIMATE**

Population Genomic approaches lead to understanding of adaptive capacity in a tree population and challenges faced in warmer climates. Majorly high-level genetic diversity and considerable phenotypic plasticity among tree species has contributed in survival through past environmental variability. However, there is need of better knowledge regarding degree of adaptation at the local level towards the climate as well as new methods of tolerance capacity prediction and adaptation to new climates. Genomic approach provides rapid identification alternatives with respect to environmental factors showing phenotypic – genotypic and environmental associations (Alberto et al., 2013; Sork et al., 2013).

Performance of genomic data compare to phenotype measurement among short-term seedling common garden was evaluated by (Mahoney et al., 2019) in addition to long-term provenance trials. They determined the adaptive variance patterns and climate features of selection using factors like bud phenology, cold hardiness and growth. About >32,000 sample SNPs for genotypes and climatic data for 281 populations were utilized (Pinus contorta). The results showed seedling phenotype markers giving better explanation of adaptive variation as compared to genomic data set or climatic data alone. GEA (genotype environment association) analysis proved better in identification of climatic factors causing diversity in cases where phenotypic data was unavailable, thus making species management easier without long-term trials.

Applied ecological genomics can help to predict the potential of evolution apparent in the local population with respect to climate change. Allele frequency shifts for adaptive Loci pertaining to climate shifts were addressed by Ingvarsson and Bernhardsson (2019) using Populous tremula (European aspen). Populous tremula was used owing to its long history available regarding its genetics, genomics and phenotype. About 94 species across 10° latitude were sequenced for the whole genome in the areas of Sweden. The data so obtained was subjected to genotype environment analysis (LFMM) and GDM modelling was done for the estimation of genetic offsets (Fitzpatrick and Keller, 2015). This resulted in the mall adaptation description of an individual having specific allelic composition when environmental shift is subjected. Large genetic adjustments were required even in a short period of nearly 50 years for specifically northern population in order to cope with their local climatic conditions as compare to the southern populations which show smaller genetic offsets and convergence with the disproportionate effects among sub artics towards climatic change (IPCC 2018).

Apart from higher focus on economically important species, there has been also studies which evaluate the influence of population genomics to realize the neutral and adaptive processes related to non-commercial but ecologically valuable species. Mayol et al. (2019), provided the evidence of adaptive divergence among growth and phonology to be correlated with the variation in temperature among provenances. The study also emphasized on the demographic decline of some species to be more pronounced as compare to others. The novel aspect of use of pathway analysis to assess the collective effect of SNPs among biological categories revealed that flavonoid biosynthesis pathway has undergone differential selection, showing the functional relevance of oxidative stress or membrane stabilization required in cold temperatures (Schultz et al., 2016). Population genomics caters a wide span of genetic considerations owing to Forest health, forest resilience and climatic change including univariate SNP – environment and SNP – phenotype associations (Kremer and Le Corre, 2012) in addition to description of adaptation in terms of poly genic process, including various loci having distinctly small effects (Boyle et al., 2017). This clears the vision of genotypic mapping process of phenotypes and provides a better understanding.

Forest management addressing climate change in the contemporary scenario is considering implementation of assisted gene flow as an important genetic tool. This is made possible with its ability to apply or increase the pre-adaptive genotype frequency in new climate (Aitken and Whitlock, 2013). Genomic data has great contribution in enriching the conservation strategies by facilitating solid estimates, owing to population adaptive variations (Funk et al., 2019). Borrell et al. (2019), reported the potential of assisted gene flow framework and its limitations in a study on Betula nana (montane dwarf birch tree). They used genotype environment association (GEA) and environmental niche modelling in order to identify the maladaptive populations that is having allele frequency deviation in current and projected future environmental conditions (c – RONA, f - RONA). Vulnerability assessment through assessment of adaptive capacity of a particular species is a very challenging task. Godbout et al. (2019), reported genomic diversity to be the expression of its environment, including climate, soil, biotic interactions and many more and how it can be used to examine adaptive capacity .

Various species of tree show hybridization with cogeners, hence contributing towards local adaptation with respect to transitional environments (Bawa and Holliday, 2016). Many tree species have been hybridized to adaptive environment that is otherwise not typical to the species range like Populous Trichocarpa X Populous balsamifera (Suarez-Gonzalez et al., 2018), Pinus Strobiformis X Pinus Flexilis (Menon et al., 2019). Sequencing in this case was done using double digest RAD sequence and combination of individual based simulations and genetic cline analysis. The results showed northward integration due to non-concordance of morphological and genomic cline center estimates. Although appearing to be degrading the biodiversity, hybridization or introgression among tree species is a natural evolutionary trajectory characteristic which provides intermediate phenotypes among ectones and by directional transfer of adaptive variations.

**GENOMIC EVOLUTION AND GENOMIC TOOLS**

Attainment of high-quality reference genomes have been difficult due to size and complexity of tree genomes. The first tree genome was sequenced in 2006 of Populus trichocarpa (Tuskan et al., 2006) and Picea Abies in 2013 (Nystedt et al., 2013). About 52 out of 200 unique plant reference genomes belong to trees species (Wegrzyn et al., 2019). The situation has been improved with the application of new genomics, bioinformatics and precision phenotypic tools. Angiosperm genomes are much easier than conifer as the later bear a large size and high repetition in genome making and is difficult to understand and work on (De La Torre et al., 2014). DNA sequencing techniques have provided important breakthroughs in case of large genomes like gymnosperms. Whole genome duplication events have characterized the evolution of angiosperms (Lee beans Mack et al., 2019). They also have higher rates of chromosomal, rearrangement and mutation rates than that of gymnosperms (Pavy et al., 2017). Adaptive evolution rates are compare using coding regions among gymnosperms and angiosperms. Lower rates of neutral evolution but higher rate of non-synonymous substitutions have been reported among gymnosperms than that of angiosperms (De La Torre et al., 2017). Gymnosperms show higher gene family expansion which is related to defense responses, climatic tolerances as well as lignin and cellulose biosynthesis. In addition to genomics the phenomic tool like UAVs which use hyperspectral sensor to create leaf spectral indices helping in responding against drought stress or pest invasions are also very useful in forest resilience, climatic control and forest health (Calderon et al., 2015). Wegrzyn et al., 2019 reported a gap between the current state of data integration for non – model species and model species. Thus implementation of the data standards, ontologies, analytical work flows and integrated databases into cyberinfrastructures and inclusion in best practices is beneficial in this context.

**CONCLUSION**

Forest health and its long-term maintenance is imperative to functioning of global ecosystem in general and to fight against climate change in particular. Trees are architects of forest ecosystem and are under challenge throughout their life span owing to biotic and abiotic stresses. There has been a rapid improvement in knowledge, owing to genomics and genetic tools as to inform forest management and conservation decision in addition to accelerating breeding programs and to take up the climate change challenges. In order to get acceptance by various stakeholders from different public decisions making authorities, a genetic tool, economic and ecologically low at cost and high at benefits should be taken into account. Genomic tools are highly versatile and provide the insight of the plant’s history and this is one of the important criteria.

**REFERENCES**

* Franklin JF, Shugart HH, Harmon ME (1987) Tree death as an ecological process. Bioscience 37:550–556. doi:10.2307/1310665
* Teale SA, Castello JD (2011) Regulators and terminators: the im- portance of biotic factors to a healthy forest. In: Castello JD, Teale SA (eds) Forest health. An integrated perspective. Cambridge University Press, Cambridge, pp 81–11 4
* Hansen EM (1999) Disease and diversity in forest ecosystems. Australas Plant Pathol 28:313–319
* Hansen EM, Goheen EM (2000) Phellinus weirii and other native root pathogens as determinants of forest structure and process in western North America. Ann Rev Phytopathol 38:515–539. doi:10. 1146/annurev.phyto.38.1.515
* Carnus JM, Parrotta J, Brockerhoff E, Arbez M, Jactel H, Kremer A, Lamb D, O’Hara K, Walters B (2006) Planted forests and biodiversity. J For 104:65–77
* Lombardero MJ, Alonso-Rodríguez M, Roca-Posada EP (2012) Tree insects and pathogens display opposite tendencies to attack native vs. non-native pines. For Ecol Manag 281:121–129. doi:10. 1016/j.foreco.
* Roberge JM, Bengtsson SBK, Wulff S, Snäll T (2011) Edge creation and tree dieback influence the patch-tracking metapopulation dynamics of a red-listed epiphytic bryophyte. J Appl Ecol 48:650–658. doi:10.1111/j.1365-2664.2011.01963.x
* Cobb RC, Rizzo DM, Hayden KJ, Garbelotto M, Filipe JAN, Gilligan CA, Dillon WW, Meentemeyer RK, Valachovic YS, Goheen E, Swiecki TJ, Hansen EM, Frankel SJ (2013) Biodiversity conservation in the face of dramatic forest disease: an integrated conservation strategy for tanoak (Notholithocarpus densiflorus) threatened by Sudden Oak Death. Madrono 60:151–164. doi:10.3120/0024-9637-60.2.151
* Cahill DM, Rookes JE, Wilson BA, Gibson L, McDougall KL (2008) Phytophthora cinnamomi and Australia’s biodiversity: impacts, predictions and progress towards control. Aust J Bot 56:279–310. doi:10.1071/BT07159
* Davis RA, Valentine LE, Craig MD, Wilson B, Bancroft WJ, Mallie M (2014) Impact of Phytophthora-dieback on birds in Banksia woodlands in southwest Western Australia. Biol Conserv 171: 136–144. doi:10.1016/j.biocon.
* MacDonald WL (2003) Dominating North American forest pathology issues of the 20th century. Phytopathology 93:1039–1040. doi:10.1094/PHYTO.2003.93.8.1039
* Hepting GH, Cowling EB (1977) Forest pathology: unique features and prospects. Ann Rev Phytopathol 15:431–450. doi:10.1146/ annurev.py.15.090177.002243
* Petrokofsky G, Brown ND, Hemery GE, Woodward S, Wilson E, Weatherall A, Stokes V, Smithers RJ, Sangster M, Russell K, Pullin AS, Price C, Morecroft M, Malins M, Lawrence A, Kirby KJ, Godbold D, Charman E, Boshier D, Bosbeer S, Arnold JEM (2010) A participatory process for identifying and prioritizing policy-relevant research questions in natural resource management:a case study from the UK forestry sector. Forestry 83:357–367. doi:10.1093/forestry/cpq018
* Wingfield MJ (1990) Current status and future prospects of forest pathology in South Africa. South Afr J Sci 86:60–62
* Holdenrieder O (2000) Zur Situation der Forstpathologie in Europa. Nachr Deut Pflanzensch 52:135–139
* Gadoury DM, Andrews J, Baumgartner K, Burr TJ, Kennelly MM, Lichens-Park A, MacDonald J, Savary S, Scherm H, Tally A, Wang GL (2009) Disciplinary, institutional, funding, and demographic trends in plant pathology: what does the future hold for the profession? Plant Dis 93:1228–1237. doi:10.1094/PDIS-93-12-1228
* MacDonald J, Allen C, Gadoury D, Jacobi W, Kelemu S, Moyer J, Murray T, Ong K, Pearson C, Sherwood J, Vidaver A (2009) Education in plant pathology: present status and future challenges. Plant Dis 93:1238–1251. doi:10.1094/PDIS-93-12-1238
* Hamelin RC (2012) Contributions of genomics to forest pathology. Can J Plant Pathol 34:20–28. doi:10.1080/07060661.2012.665389
* Wood L, Gebhardt P (2013) Bioinformatics goes to school—new avenues for teaching contemporary biology. PLoS Comp Biol 9: e1003089. doi:10.1371/journal.pcbi.1003089
* Holdenrieder O, Pautasso M, Weisberg P, Lonsdale D (2004) Tree diseases and landscape processes: the challenge of landscape pathology. Trends Ecol Evol 19:446–452. doi:10.1016/j. tree.2004.06.003
* Hatala JA, Dietze MC, Crabtree RL, Kendall K, Six D, Moorcroft PR (2011) An ecosystem-scale model for the spread of a host- specific forest pathogen in the Greater Yellowstone Ecosystem. Ecol Appl 21:1138–1153. doi:10.1890/09-2118.1
* Sieber TN (2007) Endophytic fungi in forest trees: are they mutu- alists? Fungal Biol Rev 21:75–89. doi:10.1016/j.fbr.2007.05.004
* Witzell J, Martín JA, Blumenstein K (2014) Ecological aspects of endophyte-based biocontrol of forest diseases. In: Verma VC, Gange AC (eds) Advances in endophytic research. Springer, Berlin, pp 321–333. doi:10.1007/978-81-322-1575-2\_17
* Orwig DA (2002) Ecosystem to regional impacts of introduced pests and pathogens: historical context, questions and issues. J Biogeogr 29:1471–1474. doi:10.1046/j.1365-2699.2002.00787.x
* Holzmueller EJ, Jose S, Jenkins MA (2010) Ecological conse- quences of an exotic fungal disease in eastern U.S. hardwood forests. For Ecol Manag 259:1347–1353. doi:10.1016/j.foreco. 2010.01.014
* Pautasso M, Aas G, Queloz V, Holdenrieder O (2013) European ash (Fraxinus excelsior)dieback—a conservation biology challenge. Biol Conserv 158:37–49. doi:10.1016/j.biocon.2012.08.026
* Shearer BL, Crane CE, Cochrane JA, Dunne CP (2013) Variation in susceptibility of threatened flora to Phytophthora cinnamomi. Australas Plant Pathol 42:491–502. doi:10.1007/s13313-013- 0215-1
* Westbrook, J. W., Zhang, Q., Mandal, M. K., Jenkins, E. V., Barth, L. E., Jenkins, J. W., … Holliday, J. A. (2019). Optimizing genomic selection for blight resistance in American chestnut backcross populations: A tradeoff with American chestnut ancestry implies resistance is polygenic. Evolutionary Applications, 13, 31–47. https://doi.org/ 10.1111/eva.12886
* Newhouse, A. E., Polin-McGuigan, L. D., Baier, K. A., Valletta, K. E. R., Rottmann, W. H., Tschaplinski, T. J., … Powell, W. A. (2014). Transgenic American chestnuts show enhanced blight resistance and transmit the trait to T1 progeny. Plant Science, 228, 88–97.
* Safranyik, L., Carroll, A., Régnière, J., Langor, D., Riel, W., Shore, T.… Taylor, S. (2010). Potential for range expansion of mountain pine beetle into the boreal forest of North America. The Canadian Entomologist. 142, 415–442
* Cullingham, C. I., Peery, R. M., Fortier, C. E., Mahon, E. L., Cooke, J. E. K., & Coltman, D. W. (2019). Linking genotype to phenotype to identify genetic variation relating to host susceptibility in the mountain pine beetle system. Evolutionary Applications. ht tps://doi.org/10.1111/eva.12773
* Alberto, F. J., Aitken, S. N., Alia, R., González-Martínez, S. C., Hänninen, H., Kremer, A ., … Savolainen, O. (2013). Potential for evolutionar y responses to climate change – evidence from tree populations. Global Change Biology, 19, 1645–1661.
* Sork, V. L., Aitken, S. N., Dyer, R. J., Eckert, A. J., Legendre, P., & Neale, D. B. (2013). Putting the landscape into the genomics of trees: Approaches for understanding local adaptation and population responses to changing climate. Tree Genetics and Genomes, 9, 901–911.
* Mahoney, C . R ., Maclachlan, I . R ., Lind, B. M ., Yoder, J. B., Wang, T., & Aitken, S. N. (2019). Evaluating genomic data for management of local adaptation in a changing climate: A lodgepole pine case study. Evolutionary Applications, 13, 116–131. <https://doi.org/10.1111/eva.12871>
* Ingvarsson, P. K., & Bernhardsson, C. (2019). Genome-wide signatures of environmental adaptation in European aspen (Populus tremula) under current and future climate conditions. Evolutionary Applications, 13, 132–142. <https://doi.org/10.1111/eva.12792>
* Fitzpatrick, M. C., & Keller, S. R. (2015). Ecological genomics meets community-level modeling of biodiversity : Mapping the genomic landscape of current and future environmental adaptation. Ecology Letters, 18, 1–16.
* IPCC (2018). Global Warming of 1.5°C. An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. Masson- Delmotte, V., Zhai, P., Pörtner, H.O., Roberts, D., Skea, J., Shukla, P.R., … Waterfield, T. (eds.). 11 pp.
* Mayol, M., Riba, M., Cavers, S., Grivet, D., Vincenot, L., Cattonaro, F., … González-Martínez, S. C. (2019). A multiscale approach to detect selection in nonmodel tree species: Widespread adaptation despite population decline in Taxus baccata L. Evolutionary Applications, 13, 143–160. <https://doi.org/10.1111/eva.12838>
* Schulz, E., Tohge, T., Zuther, E., Fernie, A. R., & Hincha, D. K. (2016). Flavonoids are determinants of freezing tolerance and cold acclimation in Arabidopsis thaliana. Scientific Reports, 6, 34027.
* Kremer, A., & Le Corre, V. (2012). Decoupling of differentiation between traits and their underlying genes in response to divergent selection. Heredity, 108, 375–385.
* Boyle, E. A., Yang, L., & Pritchard, J. K. (2017). An expanded view of complex traits: From polygenic to Omnigenic. Cell, 169, 1177–1185. <https://doi.org/10.1016/j.cell.2017.05.038>
* Aitken, S. N., & Whitlock, M. C. (2013). Assisted gene flow to facilitate local adaptation to climate change. Annual Reviews of Ecology, Evolution, and Systematics, 44, 367–388.
* Funk, W. C., Forester, B. R., Converse, S. J., Darst, C., & Morey, S. (2019). Improving conservation policy with genomics : A guide to integrating adaptive potential into U.S. Endangered Species Act decisions for conservation practitioners and geneticists. Conservation Genetics, 20, 11 5 –1 3 4 .
* Borrell, J. S., Zohren, J., Nichols, R. A., & Buggs, R. J. A. (2019). Genomic assessment of local adaptation in dwarf birch to inform assisted gene flow. Evolutionary Applications, 13, 161–175. https://doi.org/10.1111/eva.12883
* Godbout, J., Gros-Louis, M.-C., Lamothe, M., & Isabel, I. (2019). Going with the flow : Intraspecific variation may act as a natural ally to counterbalance the impacts of global change for the riparian species Populus deltoides. Evolutionary Applications, 13, 176–194. https://doi. org/10.1111/eva.12854
* Bawa, R., & Holliday, J. A. (2016). Genomics of speciation in temperate and boreal angiosperm trees. In A. Groover, & Q. Cronk (Ed.), Comparative and evolutionary genomics of angiosperm trees (pp. 159– 177). Cham: Springer International Publishing.
* Suarez-Gonzalez, A., Hefer, C. A., Lexer, C., Douglas, C. J., & Cronk, Q. C. B. (2018). Introgression from Populus balsamifera underlies adaptively significant variation and range boundaries in P. trichocarpa. New Phytologist, 217, 416–427.
* Menon, M., Landguth, E., Leal-Saenz, A., Bagley, J. C., Schoettle, A. W., Wehenkel, C., … Eckert, A. J. (2019). Tracing the footprints of a moving hybrid zone under a demographic history of speciation with gene flow. Evolutionary Applications, 13, 195–209. https://doi. org/10.1111/eva.12795
* Tuskan, G. A., DiFazio, S., Jansson, S., Bohlmann, J., Grigoriev, I., Hellsten, U., … Rokhsar, D. (2006). The genome of black cottonwood, Populus trichocarpa (Torr. & Gray). Science, 313, 1596–1604.
* Wegrzyn, J. L., Falk, T., Grau, E., Buehler, S., Ramnath, R., & Herndon, N. (2019). Cyberinfrastructure and resources to enable an integrative approach to studying forest trees. Evolutionary Applications, 13, 228–241. <https://doi.org/10.1111/eva.12860>
* Nystedt, B., Street, N. R., Wetterbom, A., Zuccolo, A., Lin, Y.-C., Scofield, D. G., … Jansson, S. (2013). The Norway spruce genome sequence and conifer genome evolution. Nature, 497, 579–584.
* De La Torre, A. R., Piot, A., Liu, B., Wilhite, B., Weiss, M., & Porth, I. (2019). Functional and morphological evolution in gymnosperms : A portrait of implicated gene families. Evolutionary Applications, 13, 210–227. <https://doi.org/10.1111/eva.12839>
* Leebens-Mack, J. H., Barker, M. S., Carpenter, E. J., Deyholos, M. K., Gitzendanner, M. A., Graham, S. W., … Wong, G.-K.-A. (2019). One thousand plant transcriptomes and the phylogenomics of green plants. Nature, 574, 679–685.
* Pavy, N., Lamothe, M., Pelgas, B., Gagnon, F., Birol, I., Bohlmann, J., … Bousquet, J. (2017). A high-resolution reference genetic map positioning 8.8 K genes for the conifer white spruce: Structural genomics implications and correspondence with physical distance. The Plant Journal, 90, 189–203.
* Calderon, R., Navas-Cortés, J. A., & Zarco-Tejada, P. J. (2015). Early detection and quantification of verticillium wilt in olive using hyper- spectral and thermal imagery over large areas. Remote Sensing, 7, 558 4–5610.
* Manolio, T. A., Collins, F. S., Cox, N. J., Goldstein, D. B., Hindorff, L. A., Hunter, D. J., … Visscher, P. M. (2009). Finding the missing heritability of complex diseases. Nature, 461, 747–753.
* Langlet, O. (1971). Two hundred years of genecology. Ta xo n, 20, 653–722.
* Aitken, S. N., & Bemmels, J. B. (2015). Time to get moving: Assisted gene flow of forest trees. Evolutionary Applications, 9, 271–290.
* Hamrick, J. L. (1989). Isozymes and the analysis of genetic structure in plant populations. In D. E. Soltis, P. S. Soltis, & T. R. Dudley (Eds.), Isozymes in Plant Biology (pp. 87–105). Dordrecht: Springer.
* Intergovernmental Panel on Climate Change [IPCC]. 2007. Summary for policymakers. In: Solomon, S.; Qin, D.; Manning, M.; Chen, Z.; Marquis, M.; Averyt, K.B.; Tignor, M.; Miller, H.L., eds. Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press: 1–18.
* Thrall, P. H., Burdon, J. J., & Young, A. (2001). Variation in resistance and virulence among demes of a plant host-pathogen metapopulation. *Journal of Ecology*, 736-748.
* Cantin, G., & Verdière, N. (2020). Networks of forest ecosystems: Mathematical modeling of their biotic pump mechanism and resilience to certain patch deforestation. *Ecological Complexity*, *43*, 100850.
* Kull, C. A., Ibrahim, C. K., & Meredith, T. C. (2007). Tropical forest transitions and globalization: neo-liberalism, migration, tourism, and international conservation agendas. *Society and Natural Resources*, *20*(8), 723-737.
* Namkoong, G., Boyle, T., Gregorius, H. R., Joly, H., Savolainen, O., Ratnam, W., & Young, A. (1996). *Testing criteria and indicators for assessing the sustainability of forest management: genetic criteria and indicators* (No. CIFOR Working Paper no. 10, p. 12p). Bogor: CIFOR.
* Farwig, N., Braun, C., & Böhning-Gaese, K. (2008). Human disturbance reduces genetic diversity of an endangered tropical tree, Prunus africana (Rosaceae). *Conservation genetics*, *9*, 317-326.
* Fuchs, E. J., & Hamrick, J. L. (2010). Genetic diversity in the endangered tropical tree, Guaiacum sanctum (Zygophyllaceae). *Journal of Heredity*, *101*(3), 284-291.
* Nussey, D. H., Postma, E., Gienapp, P., & Visser, M. E. (2005). Selection on heritable phenotypic plasticity in a wild bird population. *Science*, *310*(5746), 304-306.
* Millar, C. I., Stephenson, N. L., & Stephens, S. L. (2007). Climate change and forests of the future: managing in the face of uncertainty. *Ecological applications*, *17*(8), 2145-2151.
* Ledig, F. T., & Kitzmiller, J. H. (1992). Genetic strategies for reforestation in the face of global climate change. *Forest Ecology and Management*, *50*(1-2), 153-169.
* Halpin, P. N. (1997). Global climate change and natural‐area protection: management responses and research directions. *Ecological Applications*, *7*(3), 828-843.
* Bürger, R., & Lynch, M. (1995). Evolution and extinction in a changing environment: a quantitative‐genetic analysis. *Evolution*, *49*(1), 151-163.
* Bradshaw, A. D. (1991). The Croonian Lecture, 1991. Genostasis and the limits to evolution. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *333*(1267), 289-305.
* Reusch, T. B., Ehlers, A., Hämmerli, A., & Worm, B. (2005). Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences*, *102*(8), 2826-2831.
* Etterson, J. R. (2004). Evolutionary potential of Chamaecrista fasciculata in relation to climate change. I. Clinal patterns of selection along an environmental gradient in the Great Plains. *Evolution*, *58*(7), 1446-1456.
* Schaberg, P. G., DeHayes, D. H., Hawley, G. J., & Nijensohn, S. E. (2008). Anthropogenic alterations of genetic diversity within tree populations: Implications for forest ecosystem resilience. *Forest ecology and management*, *256*(5), 855-862.
* Gunderson, L. H. (2000). Ecological resilience—in theory and application. *Annual review of ecology and systematics*, *31*(1), 425-439.
* Müller-Starck, G., Ziehe, M., & Schubert, R. (2005). Genetic diversity parameters associated with viability selection, reproductive efficiency, and growth in forest tree species. In *Forest diversity and function: Temperate and boreal systems* (pp. 87-108). Berlin, Heidelberg: Springer Berlin Heidelberg.
* Thompson, I., Mackey, B., McNulty, S., & Mosseler, A. (2009). Forest resilience, biodiversity, and climate change. In *A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. Secretariat of the Convention on Biological Diversity, Montreal. Technical Series* (Vol. 43, No. 1, pp. 1-67).
* Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual review of ecology and systematics*, *4*(1), 1-23.
* Drever, C. R., Peterson, G., Messier, C., Bergeron, Y., & Flannigan, M. (2006). Can forest management based on natural disturbances maintain ecological resilience?. *Canadian Journal of Forest Research*, *36*(9), 2285-2299.
* Chapin, F. S., McGuire, A. D., Ruess, R. W., Hollingsworth, T. N., Mack, M. C., Johnstone, J. F., ... & Taylor, D. L. (2010). Resilience of Alaska’s boreal forest to climatic change. *Canadian Journal of Forest Research*, *40*(7), 1360-1370.
* Walker, B., Holling, C. S., Carpenter, S. R., & Kinzig, A. (2004). Resilience, adaptability and transformability in social–ecological systems. *Ecology and society*, *9*(2).
* Peterson, G., Allen, C. R., & Holling, C. S. (1998). Ecological resilience, biodiversity, and scale. *Ecosystems*, *1*, 6-18.
* Walker, B., & Salt, D. (2012). *Resilience practice: building capacity to absorb disturbance and maintain function*. Island press.
* Phillips, O. L., Aragão, L. E., Lewis, S. L., Fisher, J. B., Lloyd, J., López-González, G., ... & Torres-Lezama, A. (2009). Drought sensitivity of the Amazon rainforest. *Science*, *323*(5919), 1344-1347.
* Ayres, M. P., & Lombardero, M. J. (2000). Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Science of the Total Environment*, *262*(3), 263-286.
* Wilson J.B. and A.D.Q. Agnew. 1992. Positive feedback switches in plant communities. Adv. Ecol. Res. 23: 263-336
* Bonan, G.B., S. Levis, S. Sitch, M. Vertenstein and K.W. Oleson. 2003. A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamics. Global Change Biol. 9: 1543-1566.
* Callaghan, T.V., L.O. Bjorn, Y. Chernov, T. Chapin, T.R. Christensen, B. Huntley, R.A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, G. Shaver, S. Schaphoff and S. Sitch. 2004. Effects of changes in climate on landscape and regional processes, and feedbacks to the climate system. Ambio 33: 459-468.
* Betts, R., M. Sanderson, S. Woodward, Y. Malhi, T. Roberts and R.A. Betts. 2008. Effects of large-scale Amazon forest degradation on climate and air quality through fluxes of carbon dioxide, water, energy, mineral dust and isoprene. Phil. Trans. Roy. Soc. Lond. B 363: 1873-1880.
* Kellomaki, S., H. Peltola, T. Nuutinen, K.T. Korhonen and H. Strandman. 2008. Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. Phil. Trans. Roy. Soc. B: 363: 2341-2351.
* Price, D.T. and D. Scott. 2006. The Vincera project: vulnerability and impacts of North American forests to climate change: ecosystem responses and adaptation. Online: http://www.fes.uwaterloo.ca/research/ vincera/ and ftp://ftp.nofc.cfs.nrcan.gc.ca/pub/climate/dprice/vincera\_finrep\_20060601.pdf
* Berry, S.L. and M.L. Roderick. 2002. Estimating mixtures of leaf functional types using continental scale satellite and climatic data. Glob. Ecol. and Biogeogr. 11: 23–39.
* Malhi, Y., J.T. Roberts, R.A. Betts, T.J. Killeen, W.H. Li and C.A. Nobre. 2008. Climate change, deforestation, and the fate of the Amazon. Science 319: 169-172.
* Olesen, J.E., T.R. Carter, C.H. Az-Ambrona, S. Fronzek, T. Heidmann, T. Hickler, T. Holt, M. Quemeda, M. Ruiz-Ramos, G.H. Rubeak, F. Sau, B. Smith and M.T. Sykes. 2007. Uncertainties in projected impacts of climate change on European agriculture and terrestrial ecosystems. Climatic Change 81: 123-143.
* Kueppers, L. M., Southon, J., Baer, P., & Harte, J. (2004). Dead wood biomass and turnover time, measured by radiocarbon, along a subalpine elevation gradient. *Oecologia*, *141*, 641-651.
* Jiao, N. Z., Chen, D. K., Luo, Y. M., Huang, X. P., Zhang, R., Zhang, H. B., ... & Zhang, F. (2015). Climate change and anthropogenic impacts on marine ecosystems and countermeasures in China. *Advances in Climate Change Research*, *6*(2), 118-125.
* Friberg, N., Bonada, N., Bradley, D. C., Dunbar, M. J., Edwards, F. K., Grey, J., ... & Woodward, G. U. Y. (2011). Biomonitoring of human impacts in freshwater ecosystems: the good, the bad and the ugly. In *Advances in ecological research* (Vol. 44, pp. 1-68). Academic press.