

ABSTRACT

BARNES, JESSICA CAVIN. Engineering conservation: The biogeography, biopolitics, and biotechnology of American chestnut restoration. (Under the direction of Dr. Jason A. Delborne).

Given the scale and speed of contemporary environmental changes, intensive conservation interventions are increasingly being proposed that would help ecosystems and the services they provide keep pace with abiotic and biotic changes precipitated by anthropogenic activity. Ranging from assisted colonization and rewilding to facilitated adaptation and de-extinction, these efforts have been collectively and broadly referred to as *resurrection science*. Advances in genetics and genomics have opened new avenues for resurrection science and revolutionized the potential for directly manipulating the genetic composition of threatened populations in order to save them. These technologies are blurring battlelines in the wilderness debate, unearthing new dimensions of what constitutes a species, igniting new controversies over the scope of appropriate human intervention in natural systems, and challenging existing legal and institutional frameworks for governing science and nature. Although no genetically engineered organism has yet been released into wild environments for conservation purposes, transgenic American chestnut (*Castanea dentata* (Marsh.) Borkh.) trees developed for restoring the functionally extinct species throughout its native range are currently positioned to be among the first.

This dissertation uses the details of efforts to reintroduce disease-resistant American chestnut trees to consider three key questions that have emerged around resurrection science more generally. ***First, how will resurrected organisms fit into contemporary and future conditions within and beyond their historical environments?*** The extent of abiotic and biotic changes that have occurred in eastern forests since the decline of American chestnut, and the changes that are expected in the next century, will likely cause shifts in the distribution of suitable habitat for the species. Chapter 2 employs species distribution modeling to explore the nature of these shifts and their implications for restoration practice. While being explicit about the limitations of modeling, especially for American chestnut, this chapter argues that species distribution models offer a valuable tool for anticipatory and adaptive conservation governance. ***Second, in what ways does the application of genetic technoscience to conservation challenge or reify***

the political economy of plant biotechnology in agriculture? Although agricultural biotechnology has been heavily critiqued as a tool of neoliberalism, the use of genetic and genomic technologies in American chestnut restoration eschews some of the defining attributes of this approach to governance. Chapter 3 explains this apparent paradox by drawing on three years of qualitative social science research and engaging with critical theory on the nature of technologies and the nature of neoliberalism. Doing so illustrates both the value and the limitations of neoliberalism as a framework for understanding nature-society relationships and points to locations for resisting the privatization, commodification, and commercialization of nature. *And third, how can responsible decisions be made about the use of genetic technologies in conservation under high levels of uncertainty, novelty, and controversy?* Drawing primarily on interviews with scientists involved in American chestnut restoration, Chapter 4 describes both key barriers to the reorientation of conservation towards the future and the ways in which the adoption of a long-term vision, the enrollment of non-experts in restoration science, the incorporation of local knowledge, and interdisciplinary engagement serve to – or could – improve the social and ecological outcomes of this and other resurrection projects.

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Engineering conservation: the biogeography, biopolitics, and biotechnology of
American chestnut restoration

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DEDICATION

For Drew, Naomi, and Vivienne

BIOGRAPHY

Jessica Cavin Barnes grew up in a small town outside of Savannah, GA among live oaks and salt marshes. She developed an interest in the complex and dynamic processes at the intersection of human and environmental systems as an undergraduate at Mercer University, where she completed bachelor's degrees in biology and sociology. She then took a scenic route to graduate school at NC State, traveling first through doctoral work in marine science and conservation, a master's degree in environmental public health, a job performing amphibian micro-dissections in a physiology lab, and a brief stint as a middle school science teacher. Drawing on these various experiences and her eclectic interests, she aims to bring an integrated and long-term perspective to questions at the nexus of emerging technologies and the governance of natural resources, especially biodiversity. In real life, she enjoys cooking and eating good food and walking in the woods with her husband and daughters.

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CHAPTER 1

BIODIVERSITY CONSERVATION IN THE ANTHROPOCENE

Introduction

Human activity is now producing a signature on the planet so unique that a new term -- the Anthropocene -- has been employed across disciplines and contexts to describe the pervasiveness of human influence on the Earth and its consequences (Malhi, 2017). The notion of the Anthropocene is highly contested (e.g. Crist, 2013), and it remains uncertain whether or not a new epoch in the geologic time scale will be formally designated. However, it has been argued that widespread use of the term has already caused shifts in the way people think about and live on the planet (Bocking, 2015; Buck, 2015), and that the phenomena it captures -- such as climate change, land conversion, biotic rearrangement, and pollution -- have already precipitated changes in Earth's physical systems expected to be detectable for millennia (Crutzen, 2002; Steffen et al., 2011). According to Williams et al. (2015), the biosphere of the Anthropocene is distinguished by the global movement of organisms and unprecedented reconfiguration of species assemblages (Young, 2014); by the tendency of human activity to shape the evolutionary trajectories of non-human species (Russell, 2003; Hendry et al., 2017); and by increasing integration of biological and technological systems (Haff, 2014). Additionally, anthropogenic influence on the landscape is believed to be ushering in the sixth mass extinction event in Earth's history (Ceballos et al., 2015).

As the timeline and geological basis for a new Anthropocene epoch continue to be debated (Waters et al., 2016), there is also substantial disagreement about what the Anthropocene means for efforts to conserve and restore the "natural" world. In the past decade, a seismic rift has appeared in the conservation community, dividing those who maintain staunch commitments to the protection and creation of "wilderness" (Wuerthner et al., 2014; Miller et al., 2014) from those who call for acceptance and embrace of a "post-wild" world (Kareiva et al., 2012; Lorimer, 2015; Marris, 2013). These conflicting approaches to conservation are delineated by fundamental differences in perspective on dynamism, the meaning and value of naturalness, and the place of humans in Earth's systems. However,

scholars and practitioners on both sides of this schism have proposed intensive interventions -- and in some cases, have implemented them -- to help ecosystems and the services they provide keep pace with abiotic and biotic changes precipitated by anthropogenic activity. Ranging from assisted colonization (Hoegh-Guldberg et al., 2008) and rewilding (Donlan et al., 2006) to facilitated adaptation (Thomas et al., 2013) and de-extinction (Sherkow and Greely, 2013), these efforts have been collectively and broadly referred to as *resurrection science* -- the science and practice of reviving, reintroducing, and restoring threatened or extinct species and ecosystems (O'Connor, 2015). Author M. R. O'Connor (2015: 9) has described resurrection science as the wide range of activities -- often extreme -- that conservationists undertake as they “discover, study, track, hunt, love, obsess, philosophize, save, and try to resurrect” plants and “animals that are on life support today.”

Advances in genetics and genomics have opened new avenues for resurrection science and promise to revolutionize the potential for directly manipulating the genetic composition of threatened populations in order to save them (Corlett, 2017; Kumar, 2012; Johnson et al., 2016; Taylor & Gemmill, 2016). Developments in gene editing, gene drives, and synthetic biology, and related techniques such as cloning and somatic embryogenesis, have improved the ability of scientists to directly transfer adaptive alleles into at-risk populations (Thomas et al., 2013). For example, the co-optation of the CRISPR/Cas system for gene editing and gene drive promises unprecedented efficiency in both making and replicating genomic changes in target populations (Novak et al., 2018). Proposed conservation applications include the use of genetic engineering to develop tolerance to ocean warming in coral photosymbionts (Levin et al., 2017), resistance to sylvatic plague in black-footed ferrets, and resistance to *Ceratocystis* fungi in Hawaiian ‘Ohi’a trees (Novak et al., 2018). While some conservationists have argued for early exploration of the potential of these genetic technologies for addressing biodiversity loss (Corlett, 2017; Redford et al., 2013), others have specifically spoken against proposals to use them in conservation (Civil Society Working Group on Gene Drives, 2017; Webber et al., 2015). Genetic science has both revealed and deepened rifts internal to the conservation community in the past (Soulé and Mills, 1992), and it is again “wreaking philosophical havoc” (Rosner, 2013) on the field with these new techniques for

deciphering and manipulating the genetic content of wild populations. These technologies are blurring battlelines in the wilderness debate (Nelson & Callicott, 2008), drawn by those with opposing perspectives on the Anthropocene. They are also unearthing new dimensions of what constitutes a species, deepening controversies over the scope of appropriate human intervention in natural systems, and challenging existing legal and institutional frameworks for governing science, technology, and nature.

Attention to the application of genetic technologies in biodiversity conservation is growing rapidly in both academic and popular press, as scholars and journalists continue to expound upon the ethical, ecological, biological, political, and practical dimensions of de-extinction, re-wilding, and engineered genetic rescue (e.g. Bennett et al., 2017a; Davis & Moran, 2016; Minter, 2014; Piaggio et al., 2017; Potenza, 2018; Seddon et al., 2014). However, to date, no genetically engineered organisms have been released into the environment with the goal of forming independent, evolving populations of conservation relevance, and very few are even under active development. All projects remain hypothetical, so the discourse around them focuses largely on possibilities, rather than practices. The large-scale introduction of an engineered organism is arguably most tangible in the proposed use of transgenic American chestnut (*Castanea dentata* (Marsh.) Borkh.) trees to restore the functionally extinct species throughout its native range in the eastern United States (Powell, 2014). The chapters of this dissertation thus bring the specific ecological, technological, and political realities of American chestnut restoration to bear on the growing, but general literature on various approaches to species resurrection in the Anthropocene.

Case study: American chestnut restoration

Once abundant in forests from Maine to Georgia, American chestnut was rendered functionally extinct by an introduced fungal pathogen in the early 1900s (Freinkel, 2007). Likely imported along with Japanese chestnut trees through ports in New York and California, chestnut blight (*Cryphonectria parasitica*) colonizes and induces regional cell death in the vascular system of trees; the resulting perennial canker prevents the flow of water and nutrients throughout the tree and ultimately kills it above

the point of infection (Jacobs et al., 2013). Due to the density of American chestnut in the landscape and the lack of native resistance to the pathogen, *C. parasitica* spread rapidly throughout the entire range of American chestnut in mere decades, transforming a population of over four billion large canopy trees (Gravatt, 1949) into a population of around 400 million understory sprouts (Dalglish et al., 2015). American chestnut sprouts continue to regenerate from the root collars of old stumps, but they rarely flower and fruit before being killed by chestnut blight, which remains ubiquitous in the landscape (Paillet, 2002). While American chestnut is still relatively abundant and some portion of its gene pool still exists (Huang et al., 1998), its inferred ecological functions are believed to have stalled, and without sexual reproduction, it remains evolutionarily frozen in the early 1900s. As such, efforts to restore the species to its former dominance sit at a nexus between multiple forms of resurrection science, including ecological restoration, species reintroduction, facilitated adaptation, re-wilding, and de-extinction.

Current strategies to resurrect viable, evolving American chestnut populations include attempts at biological control using hypovirulent strains of the pathogen (Milgroom & Cortessi, 2004), as well as both intra- and interspecies breeding and trans- and cisgenic engineering of American chestnut trees (reviewed in Jacobs et al., 2013; Steiner et al., 2017). None of these approaches have yet resulted in trees ready for large-scale reintroduction, but “potentially blight-resistant” trees carrying resistance genes from Chinese chestnut have been developed through backcross breeding by The American Chestnut Foundation (TACF) and are currently planted on almost 1,200 acres across 680 locations throughout the species’ native range (TACF, 2018). Additionally, in cooperation with the New York Chapter of TACF, researchers at the State University of New York, College of Environmental Science and Forestry (SUNY-ESF) have used genetic engineering to transfer a gene from wheat into the American chestnut genome. This gene codes for an enzyme that neutralizes the destructive acid produced by *C. parasitica* and thus allows American chestnut trees carrying the gene to tolerate blight infection (Powell, 2014). Two transgenic events incorporating this gene are expected to undergo consideration for federal deregulation in the United States under the Coordinated Framework for Regulation of Biotechnology this year, with

applications for release in Canada to follow shortly thereafter (William Powell, personal communication, October 7, 2017).

Research questions

If approved for open release, the transgenic American chestnut developed at SUNY-ESF is poised to become the first genetically engineered organism released into wild environments for conservation purposes. This dissertation thus uses the American chestnut case to consider three key questions that have emerged around resurrection science more generally. *First, how will resurrected organisms fit into contemporary and future conditions within their historical environments and beyond?* Species that became threatened or extinguished in their historical ranges as a consequence of habitat loss, over-exploitation, or the introduction of a non-native pest or pathogen may still be subject to those pressures, while subsequent changes in land use, climate, and ecosystem structure may present new challenges. Anticipating the long-term availability of suitable habitat and the possible consequences of reintroducing resurrected organisms both within and beyond their native ranges is essential for successful and responsible conservation. *Second, in what ways does the application of genetic technoscience to conservation challenge and reify the political economy of plant biotechnology in agriculture?* Agricultural biotechnology has been heavily critiqued as a tool of neoliberalism, one that consistently facilitates the privatization, commodification, and commercialization of nature. However, the context of biodiversity conservation presents some resistance to neoliberalism and warrants re-examining prevailing conclusions about the neoliberal politics of genetic and genomic technologies. *And third, how can responsible decisions be made about the use of genetic technologies in conservation under high levels of uncertainty, novelty, and controversy?* Proposals to release genetically manipulated organisms into uncontrolled and shared environments are challenging existing regulatory structures for both biotechnology and endangered species. They thus necessitate the exploration and adoption of alternative frameworks for decision-making about the safety and desirability of this approach to conservation.

The following chapters draw on an interdisciplinary set of theories and methods from political ecology, science and technology studies (STS), and physical geography to approach and answer these

important questions about the governance, biogeography, and politics of resurrection science in the Anthropocene. Produced as stand-alone chapters to be revised for publication in peer-reviewed journals, they are united in their attention to bridging the gap between the critical social sciences and the applied natural sciences.

Chapter 2: Modeling the future biogeography of American chestnut and challenges for assisted evolution under climate change

Efforts to establish populations of American chestnut resistant to chestnut blight -- whether developed with backcross breeding or genetic engineering -- envision a tree that will be released to participate in natural ecological and evolutionary processes throughout its historical native range. However, as is characteristic of many reintroduction projects, academic and applied attention to chestnut reintroduction has been almost exclusively focused on the initial phases of release and establishment, with far less consideration of long-term biogeographic and evolutionary dynamics. While introgressed blight resistance has the potential to allow American chestnut to co-exist with *C. parasitica*, it is unclear whether the contemporary and future abiotic and biotic conditions of the species' historical range will be suitable for reintroduced populations. Following the guidelines of the International Union for the Conservation of Nature (IUCN, 2013), this chapter uses species distribution modeling to understand the climate requirements of American chestnut and to visualize broad, continental-scale changes in the distribution of suitable habitat for the species in response to projected changes in climate over the next century. Along the way, this chapter incorporates careful attention to the limitations of species distribution models, especially for a species like American chestnut, whose distribution was substantially altered by two introduced pathogens and continues to reflect historical, rather than contemporary, climatic conditions.

Consistent with other projections for North American tree species (e.g. Iverson et al., 2008), this model shows significant contraction of suitable habitat for American chestnut within the species' historical range and the expansion of suitable habitat in regions to the north of it by 2080. These potential shifts have a number of implications for conservation practice. In particular, they highlight the importance

of germplasm conservation, especially in southern regions where relict populations are high in genetic diversity and at greatest risk of climate-related extirpation; the value of local adaptation and potential role of facilitated adaptation to changing climatic conditions; and a need to address knowledge gaps related to the ways in which blight-resistant American chestnut might interact with other species within and outside of its native range. This chapter also broadly argues that the goals of assisted evolution projects, which often aim to maintain species in their native ranges, may need to adjust to account for the uncertainty and novelty of future environmental conditions.

Chapter 3: Resistance and restoration: Polanyi's double movement and the politics of genetic technoscience

Innovations in genetics and genomics have drawn attention from critical scholars in geography, science and technology studies (STS), sociology, and anthropology as technologies that enable the enactment and extension of neoliberal capitalism, particularly in agriculture. Many of these critiques are related to the tendency of genetic science to promote reductionism in the way we understand and interact with other organisms, including the notion that they can be simply reprogrammed through genetic modification. In agriculture, this reductionist perspective has ignored the complexity of natural systems and facilitated the privatization and commodification of plant genetic resources through patents and intellectual property protections (Busch, 2010; McAfee, 2003). But many of these patterns were described well before the use of genetic technologies in biodiversity conservation became an anticipated possibility. This new application of genetic technoscience, examined through the case of American chestnut restoration, embodies important discontinuities with neoliberal critiques of genetic technologies in agriculture. Using the theoretical lenses of Karl Polanyi's (1944) double movement and Langdon Winner's (1980) description of technological politics, this paper explains why and how social and biological systems have presented some resistance to the neoliberalization of nature. Drawing on participant observation, interviews, and historical analysis, we specifically describe how the anticipations, agency, and normative commitments of the developers of this technology, combined with the biology of American chestnut and the context of restoration, have resisted the genetic commodification of nature.

Chapter 4: Anticipatory governance and the reorientation of biodiversity conservation in the Anthropocene: lessons from American chestnut restoration

Biodiversity conservation, as a scientific field and applied practice, has historically been oriented towards the past, centrally concerned with the maintenance or recreation of pre-disturbance or “natural” conditions. However, the direction, scale, pace, and irreversibility of contemporary environmental changes, many of which are wrought by human activity, challenge conservation approaches and paradigms that are based on the preservation of historical, baseline conditions and have resulted in calls for a reorientation of conservation towards the future. This reorientation has proven difficult as it requires fundamental changes in the field’s policies, practices, and philosophies. This chapter suggests that the framework of anticipatory governance (Karinen & Guston, 2009), as developed by scholars in science and technology studies (STS), offers conservation science an approach to future-oriented decision-making that is well-equipped to consider both novel environmental conditions and novel conservation approaches that incorporate emerging genetic technologies. Defined by a combination of foresight, engagement, and integration (Barben et al., 2008) anticipatory governance is also consistent with ongoing conversations in conservation science about the need for a long-term perspective (Cook et al., 2014; Kass et al., 2011) the engagement of local communities (Sterling et al., 2017), and the inclusion of social science insights on human dimensions in conservation planning (Bennett et al., 2017b).

Drawing on three years of qualitative social science research, including participant-observation and in-depth interviews, this chapter distills three key constraints on the adoption of a future orientation by organizations involved in American chestnut restoration and then describes how these constraints have been -- or could be -- circumvented by activities that embody the dimensions of anticipatory governance. Future-oriented and long-term anticipations have been limited in American chestnut restoration by commitments to a particular vision of the historical importance of the species; practical limits in expertise and resources; and the confines of biotechnology policy. However, as scientists involved in this effort have engaged in dialogues and collaborations with public audiences and other experts, their capacity to anticipate and prepare for the social and ecological ramifications of their work has been expanded.

References

- Barben D, Fisher E, Selin C and Guston DH (2008) Anticipatory governance of nanotechnology: Foresight, engagement, and integration. In: Hackett EJ, Amsterdamska O, Lynch M and Wajcman J (eds) *The Handbook of Science and Technology Studies*. Cambridge, MA: The MIT Press, 979–1000.
- Bennett JR, Maloney RF, Steeves TE, et al. (2017a) Spending limited resources on de-extinction could lead to net biodiversity loss. *Nature Ecology & Evolution* 1: 0053. DOI: 10.1038/s41559-016-0053.
- Bennett NJ, Roth R, Klain SC, et al. (2017b) Conservation social science: Understanding and integrating human dimensions to improve conservation. *Biological Conservation* 205: 93–108. DOI: 10.1016/j.biocon.2016.10.006.
- Bocking S (2015) Ecological concepts: Seeing, placing, imposing. *Geoforum* 65: 489–492. DOI: 10.1016/j.geoforum.2015.08.014.
- Buck HJ (2015) On the possibilities of a charming Anthropocene. *Annals of the Association of American Geographers* 105(2): 369–377.
- Busch L (2010) Can fairy tales come true? The surprising story of neoliberalism and world agriculture. *Sociologia Ruralis* 50(4): 331–351. DOI: 10.1111/j.1467-9523.2010.00511.x.
- Ceballos G, Ehrlich PR, Barnosky AD, et al. (2015) Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances* 1(5): e1400253–e1400253. DOI: 10.1126/sciadv.1400253.
- Civil Society Working Group on Gene Drives (2018) A Call for Conservation with a Conscience: No Place for Gene Drives in Conservation. Available at: http://www.synbiowatch.org/wp-content/uploads/2016/09/letter_vs_genedrives.pdf (April 7, 2018)
- Cook CN, Inayatullah S, Burgman MA, et al. (2014) Strategic foresight: how planning for the unpredictable can improve environmental decision-making. *Trends in Ecology & Evolution* 29(9): 531–541. DOI: 10.1016/j.tree.2014.07.005.
- Corlett RT (2017) A Bigger Toolbox: Biotechnology in Biodiversity Conservation. *Trends in Biotechnology* 35(1): 55–65. DOI: 10.1016/j.tibtech.2016.06.009.
- Crist E (2013) On the poverty of our nomenclature. *Environmental Humanities* 3(1): 129–147.
- Crutzen PJ (2002) Geology of mankind. *Nature* 415(6867): 23–23.
- Dalgleish H, Nelson C, Scrivani J, et al. (2015) Consequences of Shifts in Abundance and Distribution of American Chestnut for Restoration of a Foundation Forest Tree. *Forests* 7(1): 4. DOI: 10.3390/f7010004.
- Davis CN and Moran MD (2016) An argument supporting de-extinction and a call for field research. *Frontiers of Biogeography* 8(3). DOI: 10.21425/F58328431.

- Donlan CJ, Berger J, Bock CE, et al. (2006) Pleistocene Rewilding: An Optimistic Agenda for Twenty-First Century Conservation. *The American Naturalist* 168(5): 660–681. DOI: 10.1086/508027.
- Freinkel S (2007) *American chestnut: the life, death, and rebirth of a perfect tree*. Berkeley: University of California Press.
- Gravatt F (1949) Chestnut blight in Asia and North America. *Unasylva* 3: 2–7.
- Haff PK (2014) Technology as a geological phenomenon: implications for human well-being. *Geological Society, London, Special Publications* 395(1): 301–309. DOI: 10.1144/SP395.4.
- Huang H, Dane F and Kubisiak T (1998) Allozyme and RAPD analysis of the genetic diversity and geographic variation in wild populations of the American chestnut (Fagaceae). *American Journal of Botany* 85(7): 1013–1013.
- Hendry AP, Gotanda KM and Svensson EI (2017) Human influences on evolution, and the ecological and societal consequences. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372(1712): 20160028. DOI: 10.1098/rstb.2016.0028.
- Hoegh-Guldberg O, Hughes L, McIntyre S, et al. (2008) Assisted Colonization and Rapid Climate Change. *Science* 321(5887): 345–346. DOI: 10.1126/science.1157897.
- IUCN (2013) Guidelines for reintroductions and other conservation translocations, Version 1.0. IUCN Species Survival Commission, Gland, Switzerland
- Iverson L, Prasad A, Matthews S (2008) Modeling potential climate change impacts on the trees of the northeastern United States. *Mitigation and Adaptation Strategies for Global Change* 13:487–516. <https://doi.org/10.1007/s11027-007-9129-y>
- Jacobs DF, Dalgleish HJ and Nelson CD (2013) A conceptual framework for restoration of threatened plants: the effective model of American chestnut (*Castanea dentata*) reintroduction. *New Phytologist* 197(2): 378–393. DOI: 10.1111/nph.12020.
- Johnson JA, Altwegg R, Evans DM, et al. (2016) Is there a future for genome-editing technologies in conservation? *Animal Conservation* 19(2): 97–101. DOI: 10.1111/acv.12273.
- Kareiva P, Marvier M, Lalasz R (2012) Conservation in the anthropocene: beyond solitude and fragility. *Breakthrough Journal* 2. Available at: <https://thebreakthrough.org/index.php/journal/past-issues/issue-2/conservation-in-the-anthropocene> (April 10, 2018)
- Karinen R and Guston DH (2009) Toward Anticipatory Governance: The Experience with Nanotechnology. In: Kaiser M, Kurath M, Maasen S, et al. (eds) *Governing Future Technologies*. Dordrecht: Springer Netherlands, pp. 217–232. DOI: 10.1007/978-90-481-2834-1_12.
- Kass GS, Shaw RF, Tew T, et al. (2011) Securing the future of the natural environment: using scenarios to anticipate challenges to biodiversity, landscapes and public engagement with nature: Scenarios and the natural environment. *Journal of Applied Ecology* 48(6): 1518–1526. DOI: 10.1111/j.1365-2664.2011.02055.x.
- Kumar S (2012) Extinction need not be forever. *Nature News* 492(7427): 9.

- Levin RA, Voolstra CR, Agrawal S, et al. (2017) Engineering Strategies to Decode and Enhance the Genomes of Coral Symbionts. *Frontiers in Microbiology* 8: 1220. DOI: 10.3389/fmicb.2017.01220.
- Lorimer J (2015) *Wildlife in the Anthropocene: conservation after nature*. Minneapolis: University of Minnesota Press.
- Malhi Y (2017) The Concept of the Anthropocene. *Annual Review of Environment and Resources* 42: 77–104.
- Marris E (2013) *Rambunctious garden: saving nature in a post-wild world*. New York: Bloomsbury.
- McAfee K (2003) Neoliberalism on the molecular scale: Economic and genetic reductionism in biotechnology battles. *Geoforum* 34(2): 203–219. DOI: 10.1016/S0016-7185(02)00089-1.
- Miller B, Soulé ME and Terborgh J (2014) ‘New conservation’ or surrender to development? *Animal Conservation* 17(6): 509–515. DOI: 10.1111/acv.12127.
- Milgroom MG and Cortesi P (2004) Biological control of chestnut blight with hypovirulence: A critical analysis. *Annual Review of Phytopathology* 42(1): 311–338. DOI: 10.1146/annurev.phyto.42.040803.140325.
- Minteer B (2014) Is it right to reverse extinction? *Nature* 509(7500): 261–262.
- Nelson MP and Callicott JB (eds.) (2008) *The wilderness debate rages on: Continuing the great new wilderness debate*. Athens: University of Georgia Press
- Novak BJ, Maloney T and Phelan R (2018) Advancing a New Toolkit for Conservation: From Science to Policy. *The CRISPR Journal* 1(1): 11–15. DOI: 10.1089/crispr.2017.0019.
- O'Connor MR (2015) *Resurrection science: Conservation, de-extinction and the precarious future of wild things*. New York: St. Martin's Press.
- Paillet FL (2002) Chestnut: history and ecology of a transformed species. *Journal of Biogeography* 29(10–11): 1517–1530. DOI: 10.1046/j.1365-2699.2002.00767.x
- Piaggio AJ, Segelbacher G, Seddon PJ, Alphey L, Bennett EL, Carlson RH, Friedman RM, Kanavy D, Phelan R, Redford KH, and Rosales M (2017) Is it time for synthetic biodiversity conservation? *Trends in ecology & evolution* 32(2): 97–107.
- Polanyi K (1944) *The Great Transformation: The Political and Economic Origins of Our Time*. Boston: Beacon Press.
- Potenza A (2018, April 6) Inside the high-tech plot to save the Northern White Rhino from extinction. *The Verge*. Available at: <https://www.theverge.com/2018/4/6/17175936/northern-white-rhino-de-extinction-stem-cells-sudan> (April 8, 2017)
- Powell W (2014) The American chestnut's genetic rebirth. *Scientific American* 310(3): 68–73. DOI: 10.1038/scientificamerican0314-68.

- Redford KH, Adams W and Mace GM (2013) Synthetic Biology and Conservation of Nature: Wicked Problems and Wicked Solutions. *PLoS Biology* 11(4): e1001530. DOI: 10.1371/journal.pbio.1001530.
- Rosner, H. (2013). Is conservation extinct? A new look at preserving biodiversity. *Ensia*. Retrieved from <http://ensia.com/features/is-conservation-extinct/> (April 7, 2018)
- Russell E (2003) Evolutionary History: Prospectus for a New Field. *Environmental History* 8(2): 204. DOI: 10.2307/3985709.
- Seddon PJ, Moehrensclager A and Ewen J (2014) Reintroducing resurrected species: selecting DeExtinction candidates. *Trends in Ecology & Evolution* 29(3): 140–147. DOI: 10.1016/j.tree.2014.01.007.
- Sherkow JS and Greely HT (2013) What if extinction is not forever? *Science* 340(6128): 32-23.
- Soulé ME and Mills LS (1992) Conservation genetics and conservation biology: a troubled marriage. Conservation of biodiversity for sustainable development. Scandinavian University Press, Oslo. 1992:55-69.
- Steffen W, Grinevald J, Crutzen P, et al. (2011) The Anthropocene: conceptual and historical perspectives. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 369(1938): 842–867. DOI: 10.1098/rsta.2010.0327.
- Steiner KC, Westbrook JW, Hebard FV, Georgi LL, Powell WA, and Fitzsimmons SF (2016) Rescue of American chestnut with extraspecific genes following its destruction by a naturalized pathogen. *New Forests* 48:317-336. DOI: 10.1007/s11056-016-9561-5.
- Sterling EJ, Betley E, Sigouin A, Gomez A, Toomey A, Cullman G, et al. (2017) Assessing the evidence for stakeholder engagement in biodiversity conservation. *Biological Conservation*, 209, 159–171. DOI: 10.1016/j.biocon.2017.02.008
- Taylor HR, Gemmill NJ (2016) Emerging Technologies to Conserve Biodiversity: Further Opportunities via Genomics. Response to Pimm et al. *Trends in ecology & evolution* 31(3): 171-172.
- The American Chestnut Foundation (TACF) (2018) Regional breeding. Available at: <https://www.acf.org/our-work/regional-breeding/> (April 8, 2018)
- Thomas MA, Roemer GW, Donlan CJ, et al. (2013) Gene tweaking for conservation. *Nature* 501: 485–486.
- Waters CN, Zalasiewicz J, Summerhayes C, et al. (2016) The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science* 351(6269): aad2622–aad2622. DOI: 10.1126/science.aad2622.
- Webber BL, Raghu S and Edwards OR (2015) Is CRISPR-based gene drive a biocontrol silver bullet or global conservation threat? *Proceedings of the National Academy of Sciences* 112(34): 10565–10567. DOI: 10.1073/pnas.1514258112.

Williams M, Zalasiewicz J, Haff PK, et al. (2015) The Anthropocene biosphere. *The Anthropocene Review* 2(3): 196–219.

Winner L (1980) Do Artifacts Have Politics? *Daedalus* 109(1): 121-136.

Wuerthner G, Crist E, and Butler T (eds.). *Keeping the wild: against the domestication of Earth*. Washington: Island Press.

Young KR (2014) Biogeography of the Anthropocene Novel species assemblages. *Progress in Physical Geography* 38(5): 664–673. DOI: 10.1177/0309133314540930.

CHAPTER 2

MODELING THE FUTURE BIOGEOGRAPHY OF AMERICAN CHESTNUT AND CHALLENGES FOR ASSISTED EVOLUTION UNDER CLIMATE CHANGE

Abstract

Given the scale and speed of contemporary environmental changes, intensive conservation interventions are increasingly being proposed that would assist the evolution of adaptive traits in threatened species. The ambition of these projects is tempered by a number of concerns, including the potential maladaptation of manipulated organisms for contemporary and future climatic conditions in their historical ranges. Following the guidelines of the International Union for the Conservation of Nature, we use a species distribution model (SDM) to consider the potential impact of climate change on the distribution and quantity of suitable habitat for American chestnut (*Castanea dentata* (Marsh.) Borkh.), a functionally extinct forest species that has been the focus of various restoration efforts for over 100 years. Today, efforts to release blight-resistant American chestnut trees developed through backcross breeding and genetic engineering are positioned to be one of the first range-wide experiments in assisted evolution. Consistent with other SDMs for North American trees, our model shows contraction of suitable habitat for American chestnut within the species' historical range and the expansion of suitable habitat in regions to the north of it by 2080. These broad changes have significant implications for restoration practice; in particular, they highlight the importance of germplasm conservation, local adaptation, and addressing knowledge gaps about the interspecific interactions of American chestnut. More generally, this model demonstrates that the goals of assisted evolution projects, which often aim to maintain species in their native ranges, may need to adjust to account for the uncertainty and novelty of future environmental conditions.

Introduction

The scale and speed of contemporary environmental changes attributable to processes like climate change, land conversion, biotic rearrangement, and pollution challenge the adaptive limits of many organisms; they do not have enough plasticity to deal with these new threats, dispersal capacity to escape them, or time to adapt to them evolutionarily (Merila and Hendry 2014). Under these conditions, intensive conservation interventions have been proposed -- and in some cases, are being implemented -- to help species keep pace with new abiotic or biotic conditions. For decades, efforts have been focused on translocations (Seddon 2010) and assisted colonization (Hoegh-Guldberg et al. 2008) -- strategies that help organisms evade new pressures by relocating them to more suitable habitat. More recently, attention has turned to strategies that expedite the adaptation of threatened plant or animal populations to new conditions within their native ranges by inducing targeted and heritable genetic or epigenetic changes (Johnson et al. 2016; Jones and Monaco 2009; Thomas et al. 2013; van Oppen et al. 2015). Broadly referred to as *(human-)assisted evolution*, these approaches may make use of relatively standard techniques like selective breeding, mutation, and hybridization or employ emerging techniques such as acclimatization, microbiome manipulation, and genetic engineering (Schlaepfer et al 2005; van Oppen et al. 2015). Proposed applications include selectively breeding corals within or across species to facilitate adaptation to ocean warming (van Oppen et al. 2014, 2015); editing the genomes of Hawaiian ‘Ohi’a trees for resistance to *Ceratocystis* fungi (Novak et al. 2018); and modifying the skin microbiome of amphibians to enhance resistance to chytrid fungus (Bletz et al. 2013). Though diverse in target species and approach, most assisted evolution projects have a shared goal: establishing self-sustaining, wild populations with evolutionary potential, usually within or throughout their historical native ranges.

While the potential for assisted evolution to transform biodiversity conservation is great, so are the concerns that have been raised regarding the manipulation of wild organisms, especially using biotechnology (Laikre 2010; Muir and Howard 2004; Tiedje et al. 1989). Central among the limitations noted by ecologists is the potential for mismatch between the traits of manipulated organisms and their recipient ecosystems; these organisms may be unfit for current conditions in their historical environments

or overly competitive among conspecifics within or beyond their native ranges. These biogeographic concerns have been discussed at length in the context of conservation reintroductions and translocations (Osborne and Seddon 2012), and their relevance for de-extinction candidates has recently been described (Peers et al. 2016; Robert et al. 2016; Seddon et al. 2014). They also carry particular weight for the targets of assisted evolution. These are often species that have become “trapped” by novel conditions and, whether due to local, regional, or functional extinction or a reduction in sexual reproduction, have not evolved along with their biophysical environments for some time (Schlaepfer et al. 2002, 2005). While assisted evolution techniques can be used to introgress particular adaptive traits, changes in land use, climate, and ecosystem structure since the decline of the species may present additional challenges to their long-term restoration.

Because climatic conditions pose significant constraints on species distributions (Mackey and Lindenmeyer 2001; Woodward and Williams 1987), and given the nature of climate change projections over the next century (IPCC 2014), anticipating potential shifts in the distribution of climatically suitable habitat is particularly important for the appropriate reintroduction of organisms for conservation or ecological restoration (Falk and Millar 2016). This is especially true for species with long lifespans, delayed reproductive maturity, and limited ability to migrate to track changes in climate. The International Union for the Conservation of Nature (IUCN) (2013) suggests the use of species distribution models (SDMs) to understand the climate requirements of species targeted for reintroduction or translocation, and to project the availability of climatically suitable habitat for those species now and in the future. SDMs have been used extensively in biodiversity conservation for a variety of applications (Franklin 2013; Rodríguez et al. 2007), including forecasting the natural movement of species in response to climate change (Fitzpatrick et al. 2008; Thomas et al. 2004); predicting the spread of invasive species (Mainali et al. 2015); identifying appropriate sites for reintroduction within native ranges (Adhikari et al. 2012; Pearce and Lindenmayer 1998); and planning for the conservation of rare or threatened species (Vitt et al. 2010; Yang et al. 2013). However, they are less commonly used as a foresight tool in conservation, for example, to evaluate the long-term potential for successful restoration of threatened or

extirpated species or to anticipate the ecological impacts of reintroducing species that may eventually be better suited for areas outside of their native ranges (e.g. Peers et al. 2016).

Here, we navigate the limitations of SDMs and use modeling to consider long-term prospects for assisting the evolution of American chestnut (*Castanea dentata* (Marsh.) Borkh.), a forest species native to the Appalachian region of the eastern United States (Freinkel 2007; Rutkow 2012). Various strategies to protect and restore populations of this heritage species -- now functionally extinct due to widespread infection with an introduced pathogen -- have been pursued for over 100 years. In that time, groups involved in chestnut restoration have pioneered the application of new physical, chemical, biological, and even nuclear techniques to a conservation problem (Curry 2014; Freinkel 2007), and the project continues to push the frontier of species restoration with the development of resistant trees using backcross breeding and genetic engineering (Steiner et al. 2017). Efforts to establish these trees in the species' native range and former niche in Appalachian forests may be one of the first range-wide experiments in assisted evolution for conservation purposes (Schlaepfer et al. 2005; van Oppen et al. 2015), especially for plants and certainly using biotechnology. Groups involved in this work thus have a unique opportunity to establish a model for restoration practice that incorporates attention to the long-term biogeographic dynamics that may emerge at the intersection of novel conservation techniques and novel environmental conditions. The model presented here provides a first step in that direction.

Background

Assisting the evolution of American chestnut

In the early 1930s, residents of the southern Appalachian mountains felt as if the world was dying (Davis 2006). *Cryphonectria parasitica* (Murrill) Barr, or chestnut blight, had been accidentally imported into the United States on nursery stock from Japan, and the fungus was spreading rapidly, decimating populations of American chestnut, a forest canopy species that was central to both ecosystems and economies throughout the region (Freinkel 2008; Rutkow 2012). In mere decades, chestnut blight would render American chestnut functionally extinct throughout its entire native range (Griffin 2000). Today, the species persists primarily in the form of understory sprouts, which continue to regenerate from the

intact root collars of affected trees, but rarely flower and fruit before being killed back again by blight (Paillet 2002). The dramatic loss of American chestnut from the landscape of the eastern U.S. has been considered one of the greatest ecological disasters of the 20th century (Skousen et al. 2013), and it remains a prominent and oft-cited example of the consequences of human-mediated biotic rearrangement for forest health (Anagnostakis 1987).

Situated in a long history of technological approaches to chestnut blight (Curry 2014; Freinkel 2007), two techniques for assisting the evolution of blight resistance in American chestnut now show great promise for restoration of the species, which is considered attainable, though still long-term (Steiner et al. 2017). For almost four decades, the American Chestnut Foundation (TACF) has been pursuing a backcross breeding program in which crosses are made between surviving American chestnut trees and blight-resistant Chinese chestnut trees (*C. mollissima*); the hybrid progeny are then crossed back to their American parents in an attempt to transfer the blight resistance of the Chinese species while maintaining the characteristics of the American species (Burnham 1988; Hebard 2006). Trees in the latest generation of the backcross program display levels of blight resistance that are intermediate between American and Chinese resistance (Steiner et al. 2017). Through the efforts of local TACF chapters, backcross trees have been planted in 680 locations in the eastern U.S. on both public and private lands (TACF 2018). Additionally, in collaboration with the New York Chapter of TACF, researchers at the State University of New York, College of Environmental Science and Forestry (SUNY-ESF) have produced transgenic, blight-resistant American chestnut lines using a variety of genes from other plant species. Two lines carrying an oxalate oxidase gene from wheat are particularly high-performing and show higher levels of blight resistance than Asian species (Newhouse et al. 2014). These transgenic events are expected to undergo federal consideration for deregulation in the U.S. later this year, with an application for release in Canada to follow shortly thereafter (William Powell, personal communication, October 7, 2017). If approved for open release, pollen from these transgenic trees could be used to fertilize trees maintained by TACF in order to bolster the blight resistance of the backcross trees and add essential genetic diversity to the transgenic ones (Steiner et al. 2017).

While some assisted evolution projects are oriented towards the development of climatic tolerance in threatened species (e.g. van Oppen et al. 2015), attention in the hybrid and transgenic chestnut programs has been focused solely on the incorporation of blight resistance, to the exclusion of other adaptive traits that might be required for success in contemporary forests. TACF and researchers at SUNY-ESF have both recently begun to explore the potential for stacking genes for resistance to other pathogens with blight resistance, but adaptation to climatic conditions will be derived from standing genetic diversity (Steiner et al. 2017). While introgressed blight resistance has the potential to allow populations of American chestnut to coexist with chestnut blight, it remains unclear whether the contemporary and future climatic conditions of the species' historical range will be suitable for reintroduced populations. In spite of its attention to emerging technological approaches and its long-term conservation vision, the American chestnut restoration effort has not systematically considered the ways in which biogeographic dynamics may shape the success of ongoing and proposed interventions. Our goal in this paper was to develop a simple, yet robust SDM that would illustrate the potential for long-term and large-scale shifts in the distribution of climatically suitable habitat for American chestnut in the future and to consider the significance of those shifts for chestnut restoration.

Modeling American chestnut biogeography

Though widely used in land management, risk analysis, and ecological forecasting (Franklin 2013) and specifically recommended by the IUCN (2013) for conservation planning, SDMs have major, known limitations that are particularly problematic when modeling suitable habitat for American chestnut. Correlative SDMs, which relate the observed distribution of a species to known environmental conditions in order to determine the climate requirements of that species, assume that the population under study is at equilibrium with current climatic conditions (Pearson and Dawson 2003). In other words, the model assumes that the species is found in all or nearly all regions with a suitable climate and not found in regions with an unsuitable climate (Araujo and Pearson 2005). SDMs also assume that ecological relationships will be less important than climatic conditions in controlling distribution (Pearson and Dawson 2003). While American chestnut has a large range and many occurrence records -- traits that

improve SDM performance (Wisiz et al. 2008) -- those records reflect the distribution of the species in the presence of chestnut blight and another introduced pathogen, *Phytophthora cinnamomi* (Rands), both of which have substantially dislocated it (Russell 1987).

Likely imported through southern U.S. ports in the early 1800s along with exotic garden plants, *P. cinnamomi*, unlike chestnut blight, causes root rot and complete mortality in American chestnut trees (Crandall et al. 1945). *Phytophthora* infection eliminated American chestnut from previously suitable areas in Florida, Alabama, and the Piedmont of North Carolina before the 19th century and has continued to constrict the distribution of the species in other warm and low-elevation regions of its native range (Anagnostakis 2001). As a waterborne pathogen, *Phytophthora* has had a particularly large impact on American chestnut populations in areas subject to extended periods of soil saturation (Crandall et al. 1945; Rhoades et al. 2003). Climatically suitable habitat for American chestnut thus likely exists in areas where the species is no longer found. Additionally, the range of American chestnut was still expanding westward when chestnut blight was introduced (Russell 1987), so areas outside of its historical, realized range may also be suitable. While American chestnut is still relatively abundant in some places and a portion of its gene pool still exists (Huang et al. 1998), both sexual reproduction and dispersal are rare (Anagnostakis 2001). Consequently, the species remains both evolutionarily and biogeographically frozen in the early 1900s. As has been demonstrated for other long-lived plant species (Pearson and Dawson 2003; Woodward 1990), the current distribution of American chestnut likely reflects historical climate conditions as well as ecological relationships -- patterns that complicate the application of a SDM to the species.

SDMs have, however, been used a handful of times to consider the impact of climate change on American chestnut habitat at various scales. A number of large-scale projects have modeled the influence of climate change on the future distribution of temperate forest species in the U.S., including American chestnut (Iverson et al. 2008; McKenney et al. 2007; Potter et al. 2010). Given the scope of these projects, they do not account for what is known about the history or ecology of the individual species included in their analyses. Additionally, because American chestnut is currently a minor species in eastern forests,

there has been no publication of a potential future range map for the species based on these models or discussion about their significance for American chestnut restoration. Another model projected changes in the distribution and quantity of suitable habitat for American chestnut within Shenandoah National Park in response to changes in maximum temperature (Santoro 2013). While this project was focused on American chestnut restoration, the coarse resolution of the temperature data used in that study precludes a strong conclusion about the likelihood of climate-induced changes in suitable habitat on a site-level scale (Santoro 2013). Further, given large differences in how the climates in the northeastern and southeastern U.S. have changed over the past century and are expected to change in the future (Kunkel et al. 2013a, b), patterns in Shenandoah cannot be extrapolated to the rest of the species' range.

Below, we present a SDM for American chestnut that addresses the limitations of previous studies and contends with some of the more general limitations of correlative SDMs by 1) using presence-only modeling; 2) relying on occurrence data that has been thinned to correct for nonrandom sampling; 3) modeling habitat suitability on a continental scale; 4) limiting environmental variables to temperature and precipitation factors; and 5) averaging a large number of global climate models to project future habitat. The resulting model, rather than predicting the exact location of suitable habitat for American chestnut in the future, is a useful starting point for considering the long-term risks and benefits of American chestnut reintroduction and challenges for the assisted evolution of this species.

Methods

Species distribution modeling in Maxent

The distribution of suitable habitat for American chestnut was described using maximum entropy species distribution modeling in Maxent (Phillips et al. 2006). Maxent consistently outperforms other tools for niche modeling and is relatively easy to use (Merow et al. 2013). This machine-learning process relates known, georeferenced occurrence points for a species to environmental variables that characterize that geographic area in the same time period (Phillips et al. 2006). The model can then be used to calculate the likelihood of a species occurring in other locations or times given actual or projected environmental data. Although model output can be interpreted probabilistically with rigorous assumptions

and settings, it can also be used more simply as an index of habitat suitability (Merow et al. 2013). Maxent has been used to evaluate the extinction risk posed to a variety of organisms by climate change (Pearson et al. 2014) and introduced diseases (Rödder et al. 2009), and it has been specifically discussed as a valuable tool in conservation planning for threatened plant species (Kumar and Stohlgren 2009). Importantly for modeling American chestnut habitat, Maxent is a presence-only model that does not assume that the species is absent in locations where it is not currently found (Phillips et al. 2006). Use of this modeling approach thus partially manages problems related to the representativeness of the current distribution of American chestnut. Here, a Maxent model was trained on current occurrence data for American chestnut and climate data for North America, and then used to map the distribution of suitable habitat under projected future climatic conditions. Our final model reflects the average of 10 replicate runs, using a random subsample of 25 percent of the occurrence records (79 points) for testing and the remainder (240 points) for training. Otherwise, default Maxent settings were used.

Occurrence records

The historical range of American chestnut is estimated to have covered over 800,000 km², extending north from Alabama to Maine and west into Kentucky, Tennessee, Indiana, and Ohio, as well as southern Ontario (Little 1977). Naturalized plantings outside of the native range have also been established in Nova Scotia, Wisconsin, Michigan, Iowa, and other U.S. states (Russell 1987). We aimed to model suitable habitat across this continental range, since at that scale climate factors tend to dominate biotic interactions in determining species distributions, and the assumptions of correlative SDMs are more likely to hold (Pearson and Dawson 2003). In an effort to capture occurrence records for American chestnut across the entire native range, we compiled georeferenced observational data publicly available from the Global Biodiversity Information Facility (www.gbif.org) and the Forest Inventory and Analysis National Program (<http://www.fia.fs.fed.us/>). These records reflect human observations of American chestnut, as well as herbarium records. Downloaded records were cleaned to remove duplicate points and exclude those to the west of the 100th meridian, which is well outside of the native range of American chestnut, resulting in a total of 611 records. As is common with many species of conservation concern,

these records were concentrated in areas in which sampling effort has been greatest. In particular, early and ongoing survey and restoration efforts in Pennsylvania and North Carolina, as well as a large herbarium collection in Connecticut, resulted in clusters of occurrence records in those states. Because presence-only models and Maxent, in particular, assume random or representative sampling, the accuracy and practical value of model output are improved when occurrence data are processed to correct for sampling bias (Kramer-Schadt et al. 2013; Yackulic et al. 2013). In order to correct for oversampling, the ArcGIS toolbox, SDMtoolbox (Brown 2014), was used to thin spatially correlated occurrences. This process thinned points clustered in regions of low climate heterogeneity, resulting in a final dataset with 319 unique occurrence points (Figure 1).

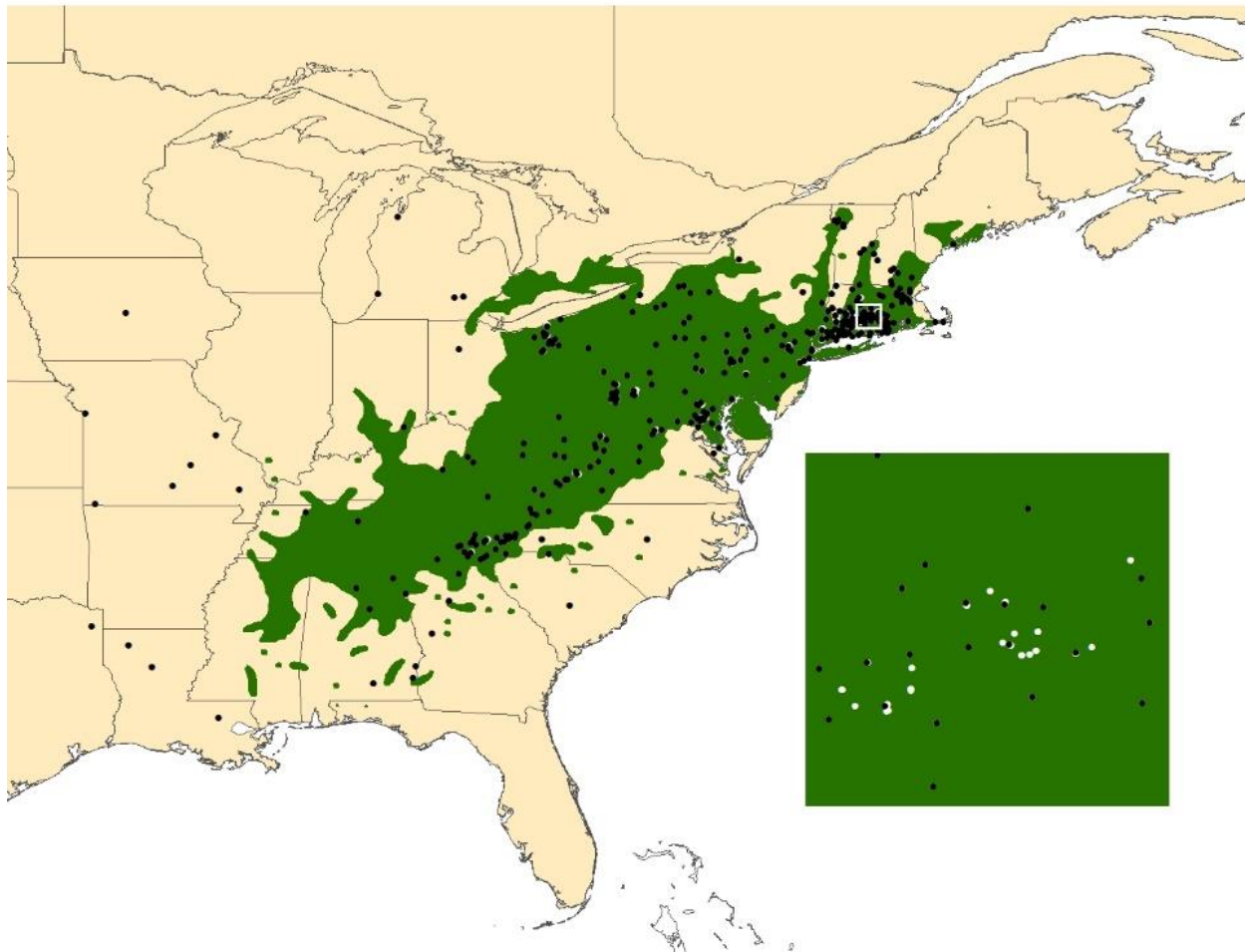


Figure 1. Occurrence records for American chestnut compiled from GBIF and FIA. Grey lines show political boundaries. Green shape shows historical range (Little 1977). White dots represent records removed during thinning. Black dots represent the 319 occurrence points used in analysis. Inset shows an example of thinning in detail.

Selection of environmental variables

Environmental variables used in this model were selected with the aim of capturing as much of the fundamental niche -- the set of conditions that foster survival and reproduction in the absence of biotic interactions (Hutchinson 1957) -- as possible. Although soil attributes and elevation are often considered key determinants of American chestnut distribution (Russell 1987; Stephenson et al. 1991), and have been used to model American chestnut habitat in other studies (Iverson et al. 2008; Santoro 2013), limitation of the species to high elevations and well-drained, xeric soils appears to reflect niche contraction in the presence of chestnut blight (Burke 2012) and *P. cinnamomi* (Rhoades et al. 2003). In fact, American chestnut is known to have been abundant in riparian areas in the southern Appalachians before the arrival of blight (Vandermast and Van Lear 2002), leading to the conclusion that it may be a generalist in terms of site conditions (Jacobs 2007), particularly in the absence of *Phytophthora*, which is most virulent in poorly-drained and compacted soils (Anagnostakis 2001; Rhoades et al. 2003). Thus, soil factors and elevation may primarily be indicators of the realized niche of American chestnut -- the geographic limits to which the species is confined due to its interaction with other organisms. In the absence of these two pathogens or given the assisted evolution of resistance to them, other elevations and soil conditions may be suitable for American chestnut, so these variables were not included in our model. Additionally, while continental-scale climate patterns are illustrative, soil attributes vary on a much smaller scale and would be needed at a finer resolution to be meaningful for restoration decisions (Rovzar et al. 2016).

In an effort to capture as much potential habitat as possible, we selected the fewest environmental variables that would provide realistic insight into the response of American chestnut to expected climatic changes. We tested the importance of 19 bioclimatic variables for American chestnut distribution, and the final model included only the four that were least correlated with each other (determined by Pearson correlation coefficients) and most explanatory of current American chestnut distribution; these were mean annual temperature (Bio1), temperature seasonality (Bio4), annual precipitation (Bio12), and precipitation seasonality (Bio15) (Table 1). Based on both historical observations and contemporary silvicultural studies, the distribution of American chestnut is known to be delimited by temperature. Historically,

American chestnut was confined both latitudinally and altitudinally by sensitivity to frost, with densities and altitudinal limits declining in the northern portions of its range (Russell 1987). Contemporary research has also demonstrated the sensitivity of American chestnut seeds, shoots, and leaves to frost damage in the northeastern U.S. (Gurney et al. 2011; Saielli et al. 2012; Schaberg et al. 2017).

Maxent also identified precipitation seasonality (Bio15) as a key variable for predicting American chestnut presence in the landscape, as indicated by its high permutation importance (Table 1). This number is determined by randomly rearranging the values of a given variable at presence and background locations and then re-assessing the ability of the model to correctly identify known occurrence locations; a large decline in model performance means that variable is important for model quality (Searcy and Shaffer 2016). Searcy and Shaffer (2016) have argued that this measure is the best reflection of the importance of environmental variables to model accuracy and may provide new insight into the ecological factors that explain species' distributions. Relatively little has been published about the relationship between American chestnut distribution and precipitation (Jacobs 2007), but the high importance of this variable indicates that American chestnut is most likely to be found in areas where precipitation is relatively consistent throughout the year -- where the difference in precipitation between the wettest and driest month is low. American chestnut growth is known to be limited in very wet and very dry soils (Russell 1987), so the importance of this variable may reflect sensitivity to both drought and saturation. Experimental studies have demonstrated physiological adaptation to water stress in American chestnut (Abrams et al. 1990; Bauerle et al. 2006); however, observed declines in the abundance of chestnut sprouts in both southwestern Virginia (Parker et al. 1993) and western North Carolina (Elliot and Swank 2008) have been partially attributed to severe drought conditions. Precipitation seasonality may also influence the distribution of American chestnut due to the relationship between soil saturation and *P. cinnamomi* infection (Rhoades et al. 2003).

Table 1. Environmental variables used in analysis and their contribution to the Maxent model.

Variable		Importance in model (permutation importance)
Annual mean temperature	(Bio1)	49.5
Temperature seasonality	(Bio4)	5.8
Annual precipitation	(Bio12)	4.2
Precipitation seasonality	(Bio15)	40.6

Climate data

Current climate data were obtained from WorldClim 1.4 ([http://www.worldclim.org/ version1](http://www.worldclim.org/version1)) and reflect averages from 1960-1990. Downscaled future climate data were obtained from the International Centre for Tropical Agriculture (CIAT) and the CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS) (<http://ccafs-climate.org/>) (Ramirez and Jarvis 2008). In this dataset, WorldClim 1.4 data were used as the baseline and processed to produce future climate layers through 2080. Current and future data were downloaded at a resolution of 2.5 minutes. The four bioclimatic variables described above were projected into the future (to 2030, 2050, and 2080) on the basis of eleven different global circulation models (GCMs) for two different representative concentration pathways (rcp): rcp 4.5 and rcp 8.5. Various GCMs have been developed by parties worldwide and embed different mathematical assumptions about the impact of carbon forcing on the atmosphere and oceans, as well as terrestrial and icy surfaces (IPCC 2014). Existing SDMs for American chestnut have used one or a few GCMs to project future climate conditions. Our choice to average a large number of GCMs acknowledges the high level of uncertainty inherent in climate modeling and accounts for large differences between individual climate models. Rcp 4.5 and rcp 8.5 are two of the greenhouse gas concentration trajectories adopted by the International Panel on Climate Change (IPCC) in its Fifth Assessment Report (IPCC 2014). These scenarios reflect a likely best- and worst-case scenario for greenhouse gas concentrations over the next century, with emissions peaking around 2040 in rcp 4.5 and continuing to increase throughout the 21st century in rcp 8.5 (IPCC 2014). Here, the GCMs were

averaged together for each future time period and rcp, resulting in six scenarios of suitable habitat in the future (under rcp 4.5 and 8.5 in 2030, 2050, and 2080).

Calculating changes in the area of suitable habitat

In order to calculate changes in the total area of climatically suitable habitat for American chestnut under future climate scenarios, the raster maps produced in the previous steps were transformed from the WGS 1984 geographic coordinate system (measured in angular degrees) to the North America Albers equal area conic projection (measured in linear meters). Then, the continuous probability values of those maps were converted into binary values representing only suitable or unsuitable habitat using SDMtoolbox (Brown, 2014). As recommended by Liu et al. (2013) for presence-only models, the maximum training sensitivity plus specificity threshold was used to delimit suitable habitat. For our model, this was one of the most inclusive thresholds, meaning it maximized the amount of potential habitat represented by the binary maps.

Results

Current distribution

Our model of the current distribution of suitable habitat for American chestnut captures much of the historical range of the species as described by Little (1977), with some notable exceptions (Figure 1). Little's range map is included here as a reference point because it is consistently used as a baseline for the American chestnut range in both research and restoration planning. The absence of suitable habitat in the southwestern part of the historical range in this model likely reflects permanent constriction of the American chestnut range in areas in which *P. cinnamomi* infection is widespread. This model also shows the availability of climatically suitable habitat outside of the historical native range, especially to the west. American chestnut moved more slowly than other hardwood species into its niche following glaciation of the American continent, and its range was still expanding to the west when chestnut blight was introduced (Russell 1987). This habitat thus likely reflects portions of the fundamental niche of American chestnut that had not yet been colonized.

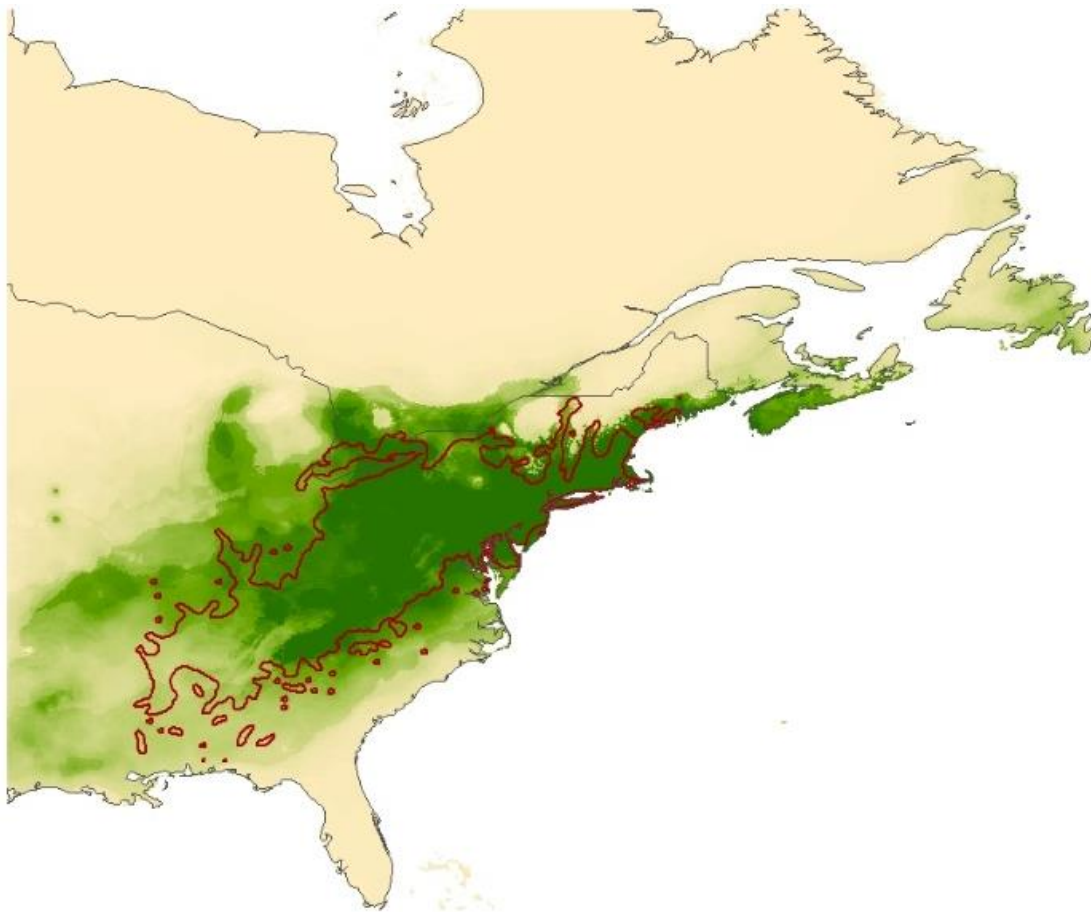


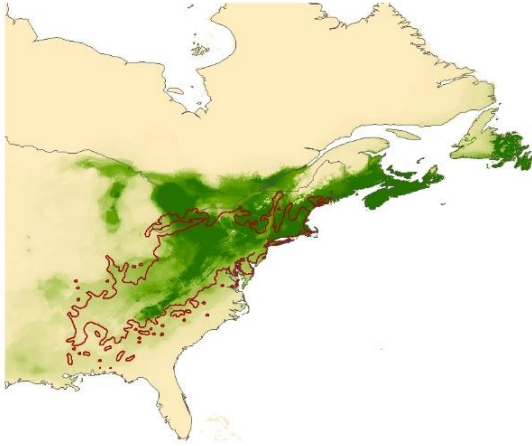
Figure 2. Species distribution model for American chestnut trained on contemporary occurrence and climate data. Darker green indicates the most suitable habitat; lighter green indicates moderately suitable habitat; and tan indicates unsuitable regions. Grey lines show political boundaries. Red line shows historical species range (Little 1977).

Future distribution

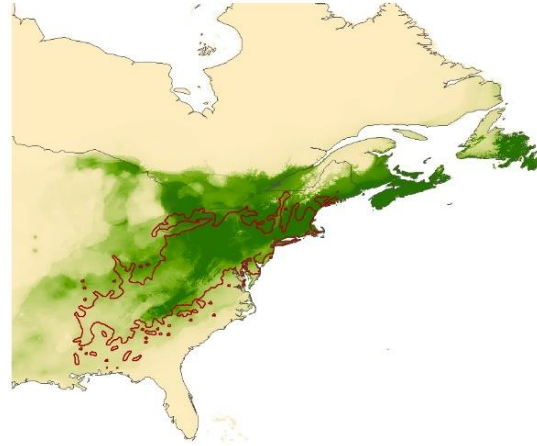
The following maps show the above species distribution model for American chestnut projected to 2030, 2050, and 2080 under the assumptions of the IPCC (2014) rcp 4.5 and rcp 8.5 scenarios. Each figure represents the average of 11 independent climate models (GCMs). In general, these figures consistently show contraction of climatically suitable habitat within the historical range of American chestnut in the U.S. and expansion of suitable habitat beyond the native range into southern and eastern Canada. Most of the climatically suitable habitat identified to the west of the species' native range becomes unsuitable in these projections. These maps also show non-linearity in the relationship between climate change projections and the distribution of suitable habitat for American chestnut. Rather than a

constant increase or decline in suitable habitat over time, this model projects fluctuations in the quantity of suitable habitat and the continual emergence of new habitat in some regions as it is lost from others. Projections based on rcp 8.5 show more drastic changes within the native range of American chestnut, with more extreme loss of suitable habitat by 2080. This scenario indicates that by 2080, climatically suitable habitat within the historical range will be primarily limited to fragments of the Appalachian core in the south and smaller portions of the mid-Atlantic and northeast. Models based on both rcp 4.5 and 8.5 project substantial expansion of climatically suitable habitat for American chestnut in Ontario and Quebec by 2080, as well as in New Brunswick, Nova Scotia, and Newfoundland.

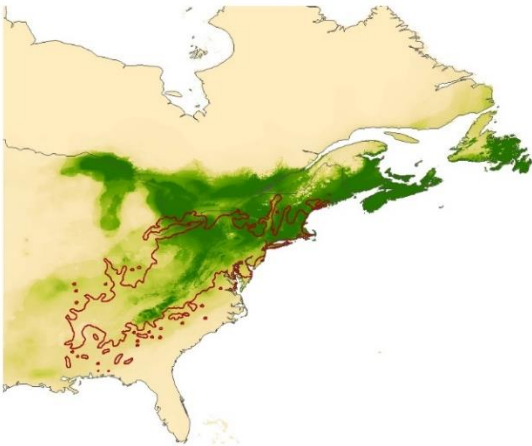
(a) 2030, rcp 4.5



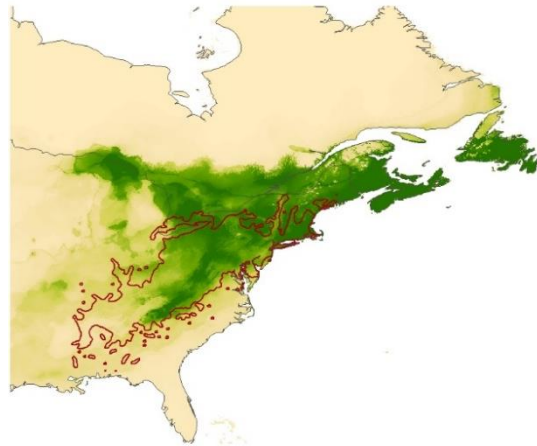
(b) 2030, rcp 8.5



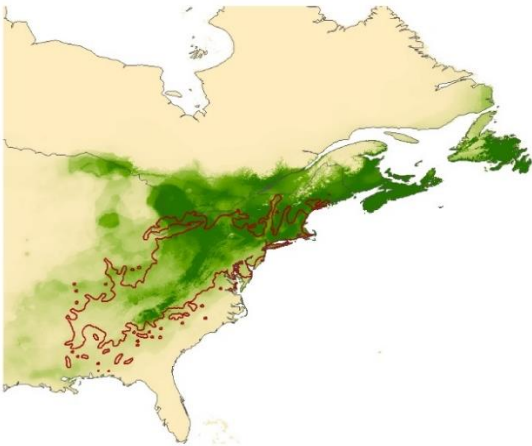
(c) 2050, rcp 4.5



(d) 2050, rcp 8.5



(e) 2080, rcp 4.5



(f) 2080, rcp 8.5

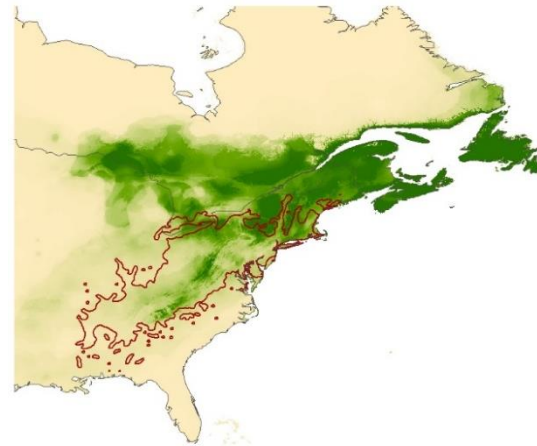


Figure 3 (a-f). Future projections of species distribution model for American chestnut. Model was projected to 2030 (2a and 2b), 2050 (2c and 2d), and 2080 (2e and 2f) under the assumptions of rcp 4.5 (2a, c, e) and rcp 8.5 (2b, d, f). Darker green indicates the most suitable habitat; lighter green indicates moderately suitable habitat; and tan indicates unsuitable regions. Grey lines show political boundaries. Red line shows historical species range (Little, 1977).

Changes in the area of suitable habitat

In our model, over 1.1 million km² in the U.S. and Canada are currently considered climatically suitable for American chestnut. It is important to keep in mind that this area, which is larger than previous estimates of the extent of the native range of American chestnut, includes all regions that are climatically suitable, whether or not they are suitable for American chestnut in terms of other abiotic or biotic conditions, including topography and land use. Additionally, this value depends heavily on the threshold selected to define suitable habitat; use of a less inclusive threshold would reduce the total area of suitable habitat. Because the same threshold was consistently used to define suitable habitat for each time period, percent differences may be more reliably illustrative of changes in habitat availability over time than estimates of absolute area. The total area of climatically suitable habitat for American chestnut is generally expected to decline over time as the amount of habitat being lost from currently suitable regions exceeds the amount of habitat being gained in new regions. However, our model projects a small, but notable increase in total area of habitat for the species by 2080 under rcp 8.5. In general, American chestnut is expected to fare better under rcp 8.5 than rcp 4.5 in terms of total available habitat, primarily due to the substantial expansion of climatically suitable habitat north of its native range in this scenario. Under both rcp 4.5 and rcp 8.5, the area of suitable habitat is expected to decline most significantly in the short-term and then increase somewhat as gains in suitable habitat compensate for habitat losses.

Table 2. Projected changes in the total area of suitable habitat for American chestnut. Calculations of total area of climatically suitable habitat for American chestnut are based on thresholded, binary output under current and future climatic conditions. Table shows differences between the current area of suitable habitat and the area of suitable habitat projected to be available under rcp 4.5 and rcp 8.5 in each future time period, as well as net gains and losses in suitable habitat relative to current conditions.

	Total km ²	Habitat difference (relative to current)		Habitat lost (relative to current)		Habitat gained (relative to current)	
		km ²	%	km ²	%	km ²	%
current	1,178,293						
<i>rcp 4.5</i>							
2030	870,220	-308,073	-26.1%	609,176	51.7%	322,792	27.4%
2050	1,031,081	-147,212	-13.6%	661,639	56.2%	536,116	45.5%
2080	984,965	-193,328	-17.3%	609,844	51.8%	438,205	37.2%
<i>rcp 8.5</i>							
2030	1,086,082	-92,211	-10.6%	434,910	36.9%	364,388	30.9%
2050	1,115,186	-63,107	-6.1%	614,654	52.2%	573,236	48.6%
2080	1,206,818	28,525	2.9%	870,086	73.8%	920,300	78.1%

Discussion

The model presented above provides a long-term and broad perspective on the ways in which the distribution of climatically suitable habitat for American chestnut may shift in response to global climate change over much of the next century. Depending on how regional climates respond to carbon forcing, significant portions of the historical range may become climatically unsuitable for American chestnut over the next 60 years. Just on the basis of climate, the species could become confined to less than half of the area that is currently suitable for it. This model thus indicates that enduring restoration of blight-resistant American chestnut throughout the native range of the species is likely not a tenable goal. New habitat for American chestnut is expected to open in much of southern Canada, however; under rcp 8.5, these gains are substantial enough to offset losses in the native range and result in an overall increase in the area of climatically suitable habitat for the species. These patterns are generally consistent with those seen in other models for American chestnut habitat described previously. In particular, models based on high-emissions scenarios consistently show virtual elimination of the most suitable habitat for American chestnut from its historical range by 2100 and significant expansion of suitable habitat in Canada. Iverson

et al. (2008) also found a complex relationship between habitat availability and climate change for American chestnut, with the total area of suitable habitat for the species expected to increase over time under a low emissions scenario, but decline under a high emissions scenario (Iverson et al. 2008). As is expected in our model for American chestnut under rcp 8.5, that project indicated that many North American tree species may experience net gains in climatically suitable habitat under climate change (Iverson et al. 2008).

In what follows, we first consider the implications of range retraction and range expansion for American chestnut reintroduction and identify some key challenges and priorities in the assisted evolution of this heritage species; then, we discuss two important limitations of the present model. As we have done throughout this paper, we maintain an emphasis on the limitations of SDMs in general and the specific challenges for modeling American chestnut habitat. This is because we agree with Millar et al. (2007, p.2145-2146), who have suggested that “[a] healthy skepticism leads us to use models to help organize our thinking, game different scenarios, and gain qualitative insight on the range of magnitudes and direction of possible future changes without committing to them as forecasts.” Our goal is to focus attention on broad and large-scale possibilities and avoid the conclusion that the present model predicts the response of complex biological systems to uncertain and multidimensional changes in future climates at any fine resolution.

Implications

The SDM presented here is not intended to predict the specific location of suitable habitat for American chestnut in the future. It does, however, provide a visual tool for considering the ways in which climate change may mediate the feasibility and desirability of intervening in the natural history of American chestnut and attempting to reintroduce this species throughout its historical range. Insofar as this model prompts scientists, conservationists, philanthropists, regulators, and others involved in American chestnut restoration to consider the potential long-term implications of their efforts, it can also facilitate the kind of future-oriented conservation and restoration planning that is increasingly called for from both natural and social scientists (Choi 2007; Willis and Birks 2006; Wyborn et al. 2016). Two

broad patterns are illuminated by the present model that carry useful insights for restoration practice: first, American chestnut is likely to lose climatically suitable habitat throughout its historical range in the eastern U.S. within this century, and, second, it is likely to gain new habitat in southern and eastern Canada.

The potential loss of climatically suitable habitat for American chestnut in its historical range is significant for reintroduction plans that depend on open crosses between backcross or transgenic trees and surviving wild trees. Rescuing the genetic diversity contained in wild sprouts is important for the future adaptive capacity of American chestnut, as the blight resistance programs of TACF and especially SUNY-ESF are based on a limited number of parental trees (Steiner et al. 2017). Our model suggests that wild trees in much of the native range may be at risk for climate-related extirpation in coming decades. TACF actively works to preserve the genetic backgrounds of surviving trees, primarily through the efforts of 16 state and multi-state chapters across the historical range of American chestnut. Chapter volunteers locate and collect germplasm from surviving trees in their areas and backcross hybrid material produced by the national organization in Meadowview, VA to these native trees (Steiner et al. 2017), creating a “living repository” of genetic diversity (Alexander et al. 2005). More recently, TACF has established a number of germplasm conservation orchards into which wild American chestnut trees are transferred for both ease of access and improved growing conditions. To date, the majority of these orchards are in Pennsylvania -- an area that our model suggests is likely to remain suitable for American chestnut in the future. However, studies indicate that the most neutral genetic diversity and rare alleles are found in American chestnut populations in the southwestern part of the species’ range (Kubisiak and Roberds 2003; Huang et al. 1998) -- an area in which American chestnut is expected to experience increasing climatic stress over the next century. Efforts in both *in situ* and *ex situ* conservation of this germplasm have been initiated (Alexander et al. 2005), and our model suggests that they should be prioritized and expanded. This work may be a valuable contribution from southern chapters that are unlikely to be situated within areas that are climatically suitable for American chestnut in the future.

The conservation of southern germplasm may also be particularly important given its adaptation to warmer climatic conditions and the apparent heritability of these adaptations in American chestnut. Genetic analyses of surviving American chestnut populations indicate that the species existed as just one metapopulation; however, genetic differentiation across altitudinal and soil gradients provides evidence of “microsite” (Steiner 2006) adaptation to local conditions, including climate (Kubisiak and Roberds 2003; Worthen et al. 2010). Silvicultural research also supports a genetic basis for regional climatic adaptation. For example, Saielli et al. (2012) found that nuts from southern American chestnut populations had lower levels of cold tolerance than those from northern populations. TACF’s state chapter structure significantly increases the level of local adaptation in the backcross breeding program, and it may eventually provide an important source of locally-adapted material that can be fertilized with pollen from transgenic, blight-resistant trees. However, local chapters largely operate within a paradigm that assumes environments to be static, rather than dynamic. Consequently, these chapters maintain relatively diverse populations of American chestnut that are well-suited to contemporary climate conditions in their regions -- or, more likely, historical conditions -- but may not be fit under future conditions. Jones and Monaco (2009) have argued that an emphasis on indigeneity in the selection of plant materials for ecological restoration may be misguided under novel environmental conditions. Instead, they suggest the incorporation of plants that are either already well-adapted or able to adapt to selective pressures in locations targeted for restoration. Given heritable thermal tolerance, TACF could facilitate crosses among surviving trees from different parts of the native range, as has been proposed for the genetic rescue of corals threatened by ocean warming (Dixon et al. 2015). Crossing individuals from remaining southern populations of American chestnut with surviving trees in other geographic regions may assist the evolution of thermal tolerance in the species, concurrent with the assisted evolution of blight and *Phytophthora* resistance.

The potential for substantial areas of climatically suitable habitat to open for American chestnut in areas north of its native range by the end of the century also has implications for restoration practice. Although Schwartz (2012) has suggested that projections of range expansion are more robust and useful for conservation planning than projections of range contraction, the ecological implications of that new

habitat are likely to be highly uncertain. Even within its native range, relatively little is known about the ecology of wild American chestnut, particularly the nature of its interactions with other plants and wildlife (Freinkel 2007; Paillet 2002). Detailed records of the pre-blight distribution of American chestnut and associated plant species are only known to exist for one plot in Connecticut; consequently, most analyses of its dispersal and migration characteristics and its community dynamics are based on surveys conducted after the decline of American chestnut began or reconstructions using chestnut stumps (Elliott & Swank 2008). Analysis of post-blight surveys along permanent transects in Coweeta Basin, NC have shown a significant increase in floral diversity following the decline of American chestnut as one dominant species was replaced by many species (Elliott & Swank 2008). Additionally, American chestnut has demonstrated the capacity to displace indigenous plant communities in a relatively short amount of time when planted outside of its native range. Nine American chestnut trees were planted from seed on a plantation in Wisconsin in the late 1800s; chestnut began to displace native oaks in a nearby woodland within 50 years and was established as a dominant canopy tree over 20 hectares within 100 years (Paillet and Rutter 1989). At present, American chestnut, which remains highly susceptible to blight infection and rarely reproduces sexually, is unlikely to pose a risk for forest communities north of its native range. However, the introgression of blight-resistance may reinstate its competitive advantage in the long-term, and widespread planting of either backcross or transgenic trees would provide abundant source material for dispersal. Given the potential for American chestnut to be a primarily Canadian species by the end of the century, filling current knowledge gaps about the ways in which blight-resistant American chestnut may interact with other Canadian forest species is essential for its responsible introduction.

Limitations

Statistician George Box famously noted that “all models are wrong, but some are useful” (Box 1979). He was referring to the ways in which models necessarily represent simplified versions of the systems they are used to investigate; they neglect certain dimensions in order to generate a manageable yet meaningful approximation of the real world (Box, 1979). Because it relies on just four climatic variables to define suitable habitat for American chestnut, the model presented here is, like all models,

wrong. It was developed and should be interpreted with awareness of the general limitations of SDMs and their specific limitations for modeling habitat for a functionally extinct species whose present distribution is a relic of its dispersal patterns in the late 19th century and its displacement by two introduced pathogens. Two limitations are especially worth noting here: first, the unavoidable conflation of biotic and abiotic constraints on the distribution of American chestnut and, second, the assumption that evolutionary processes will be negligible over the next century.

First, although Maxent is a presence-only model that minimizes the importance of missing occurrence records, in this case, a prohibitive biotic condition for American chestnut -- *Phytophthora* infection -- has historically overlapped with specific and regional abiotic conditions -- the warm temperatures and saturated soils of the Piedmont and Coastal Plain. Consequently, our model likely underestimates climatically suitable habitat in the warmer, southern portion of the species' historical range in the present, as well as any habitat represented by that climate envelope in the future. Although *P. cinnamomi* is already widespread in the U.S. under 40 degrees latitude (Balci and Bienapfl 2013), the development of root rot disease on American chestnut and other host species is thought to be limited by climatic factors, particularly low winter temperatures (Eggers et al. 2012). Under climate change, the range of *P. cinnamomi* is expected to expand and its virulence at higher latitudes and elevations is expected to increase (Bergot et al. 2004; Eggers et al. 2012). It has also been suggested that American chestnut and other trees are more susceptible to *Phytophthora* infection and root rot disease when stressed by climatic conditions (Braiser and Scott 1994; Woods 1953). Thus, without the development of American chestnut trees that are resistant to *P. cinnamomi* or otherwise protected from disease, such as through the colonization of seedlings with protective ectomycorrhizal fungi (Rhoades 2002), chestnut restoration may in fact be confined to the small portion of the species' historical range depicted as suitable by our model. In fact, the area of suitable habitat may be even further reduced as warmer temperatures and more extreme precipitation events (IPCC 2014) foster *Phytophthora* infection and spread. Both TACF and the team at SUNY-ESF have recently begun to explore the potential for adding *Phytophthora* resistance to their blight-resistant germplasm using Asian sources available in the backcross

program, an additional transgene, or a cisgene from Chinese chestnut (Steiner et al. 2017). Ultimately, although the present model cannot tease apart the influence of climate and *Phytophthora*, it does show the substantial portion of the historical range that has become unsuitable for American chestnut in the presence of this pathogen (Figure 1) and demonstrate the extent to which the introgression of *Phytophthora* resistance may increase the availability of suitable habitat for American chestnut in the future.

A second limitation emerges from the fact that SDMs are based on ecological niche theory (Pearson and Dawson 2003) and evidence that a species' niche is highly conserved over time, even in the wake of disruptive changes in climate and other environmental conditions (Wiens and Graham 2005). This allows use of the niche to understand the nature and distribution of suitable habitat for a species in the past, present, or future (Martínez-Meyer and Peterson 2006), but it also minimizes attention to evolutionary processes and the adaptive capacity of organisms (Pearson and Dawson 2003). Our model assumes that American chestnut will maintain its current niche in the future, rather than adapt to new climatic conditions, and there are reasons to both support and challenge this assumption. Based on an analysis of the bioclimatic envelopes of all chestnut species, Fei et al. (2012) concluded that the high degree of similarity in thermal tolerances among *Castanea* species indicates strong niche conservatism within the genus over tens of millions of years. Additionally, evolutionary processes are generally expected to play a smaller role for species, like American chestnut, that are long-lived and slowly dispersed (Pearson and Dawson 2003). However, experimental evidence is mounting for contemporary evolution (Stockwell et al. 2003) and the ability of populations to adapt to rapid change when they are sufficiently large and adaptive variants are present (Bell and Gonzalez 2009). Additionally, given blight and *Phytophthora* resistance and the subsequent return of sexual reproduction, the influence of both heterozygote advantage (Stilwell et al. 2003) and obligate outcrossing due to genetic self-incompatibility (McKay 1942) in American chestnut populations may facilitate higher adaptive capacity than would otherwise be expected from the small founder populations that will be used in the reintroduction of the species.

Conclusion

A century ago, residents of the southern Appalachian mountains thought the world was dying, and by some measures, it was; chestnut blight brought with it the end of a subsistence way of life that had been working for hundreds of years and a forest type that had dominated the landscape for thousands (Davis 2006; Rutkow, 2012). However, a longer-term perspective, informed by the past natural history of American chestnut, as well as scenarios of its future, reveal that American chestnut was not always a fixture in the American landscape and that it may not be possible to fully re-establish it as one. The expected long-term decline of climatically suitable habitat for American chestnut throughout its native range in the future raises important questions about the purpose and goals of its restoration, as does the potential emergence of substantial areas of new habitat outside of its range. As the social and ecological memory of American chestnut wane, efforts to resurrect it should reconsider what successful restoration means, given the novelty and uncertainty of contemporary and future environmental conditions (Jacobs et al. 2015; Redford et al. 2011; Hobbs et al. 2009). The American chestnut restoration program, though still untested on a landscape scale, remains one of the only examples of the use of assisted evolution techniques to facilitate the adaptation of a wild, forest species to an introduced pathogen. It is thus positioned to set a precedent for the assisted evolution of other species, particularly forest trees (Jacobs et al. 2013; Merkle et al 2006; Steiner et al. 2017). Those involved in this project have an opportunity to establish a model for species restoration that responds to calls for a long-term perspective in biodiversity conservation (Choi 2007; Willis and Birks 2006; Wyborn et al. 2016). As it draws attention to the biogeographic dynamics that may emerge at the intersection of novel conservation techniques and novel environmental conditions, this paper demonstrates that simple SDMs can provide a useful tool for that kind of future-oriented and anticipatory conservation practice.

References

- Adhikari D, Barik SK, Upadhaya K (2012) Habitat distribution modelling for reintroduction of *Ilex khasiana* Purk., a critically endangered tree species of northeastern India. *Ecological Engineering* 40:37–43. <https://doi.org/10.1016/j.ecoleng.2011.12.004>
- Alexander MT, Worthen LM, Craddock JH (2005) Conservation of *Castanea dentata* germplasm of the southeastern United States. *Acta Horticulturae* 485–490. <https://doi.org/10.17660/ActaHortic.2005.693.62>
- Araújo MB, Pearson RG (2005) Equilibrium of species' distributions with climate. *Ecography* 28:693–695. <https://doi.org/10.1111/j.2005.0906-7590.04253.x>
- Anagnostakis SL (1987) Chestnut blight: the classical problem of an introduced pathogen. *Mycologia* 79:23-37. <https://doi.org/10.2307/3807741>
- Anagnostakis SL (2001) The effect of multiple importations of pests and pathogens on a native tree. *Biological Invasions* 3:245–254. <https://doi.org/10.1023/A:1015205005751>
- Bauerle WL, Geoff Wang G, Bowden JD, Hong CM (2006) An analysis of ecophysiological responses to drought in American Chestnut. *Annals of Forest Science* 63:833–842. <https://doi.org/10.1051/forest:2006066>
- Balci Y, Bienapfl JC (2013) *Phytophthora* in US forests. In: Lamour K (ed) *Phytophthora*, a global perspective. CABI, Boston, pp 135-145
- Bell G, Gonzalez A (2009) Evolutionary rescue can prevent extinction following environmental change. *Ecology Letters* 12:942–948. <https://doi.org/10.1111/j.1461-0248.2009.01350.x>
- Bletz MC, Loudon AH, Becker MH, Bell SC, Woodhams DC, Minbiole KPC, Harris RN (2013) Mitigating amphibian chytridiomycosis with bioaugmentation: characteristics of effective probiotics and strategies for their selection and use. *Ecology Letters* 16:807–820. <https://doi.org/10.1111/ele.12099>
- Brown JL (2014) SDMtoolbox: a python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods in Ecology and Evolution* 5:694–700. <https://doi.org/10.1111/2041-210X.12200>
- Box GE (1979) Robustness in the strategy of scientific model building. In: Launer RL, Wilkinson GN (eds) *Robustness in statistics*. Academic Press, New York, pp 201-236
- Burke KL (2012) Niche contraction of American chestnut in response to chestnut blight. *Canadian Journal of Forest Research* 42:614–620. <https://doi.org/10.1139/x2012-002>
- Burnham CR (1988) The restoration of the American chestnut: Mendelian genetics may solve a problem that has resisted other approaches. *American Scientist* 76:478–487
- Choi YD (2007) Restoration ecology to the future: a call for new paradigm. *Restoration Ecology* 15:351–353. <https://doi.org/10.1111/j.1526-100X.2007.00224.x>

- Crandall BS, Gravatt GF, Ryan MM (1945) Root disease of *Castanea* species and some coniferous and broadleaf nursery stocks, caused by *Phytophthora cinnamomi*. *Phytopathology* 35:162–180
- Curry HA (2014) Radiation and Restoration; or, How Best to Make a Blight-Resistant Chestnut Tree. *Environmental History* 19:217–238. <https://doi.org/10.1093/envhis/emu001>
- Davis DE (2006) Historical Significance of American Chestnut to Appalachian Culture and Ecology. In: Steiner KC, Carlson JE (eds) *Restoration of American chestnut to forest lands: Proceedings of a conference and workshop*. National Park Service, Washington, DC, pp 53-60
- Dixon GB, Davies SW, Aglyamova GA, Meyer E, Bay LK, Matz MV (2015) Genomic determinants of coral heat tolerance across latitudes. *Science* 348:1460–1462. <https://doi.org/10.1126/science.1261224>
- Eggers JE, Balci Y, MacDonald WL (2012) Variation among *Phytophthora cinnamomi* isolates from oak forest soils in the eastern United States. *Plant Disease* 96:1608–1614. <https://doi.org/10.1094/PDIS-02-12-0140-RE>
- Falk DA, Millar CI (2016) The influence of climate variability and change on the science and practice of restoration ecology. In: Palmer MA, Zedler JB, Falk DA (eds) *Foundations of Restoration Ecology*. Island Press, Washington, DC, pp 484–513
- Fitzpatrick MC, Gove AD, Sanders NJ, Dunn RR (2008) Climate change, plant migration, and range collapse in a global biodiversity hotspot: the *Banksia* (Proteaceae) of Western Australia. *Global Change Biology* 14:1337-1352. <https://doi.org/10.1111/j.1365-2486.2008.01559.x>
- Franklin J (2013) Species distribution models in conservation biogeography: developments and challenges. *Diversity and Distributions* 19:1217–1223. <https://doi.org/10.1111/ddi.12125>
- Freinkel S (2007) *American chestnut: the life, death, and rebirth of a perfect tree*. University of California Press, Berkeley
- Griffin, G.J. 2000. Blight control and restoration of the American chestnut. *Journal of Forestry* 98(2):22–27
- Gurney KM, Schaberg PG, Hawley GJ, Shane JB (2011) Inadequate cold tolerance as a possible limitation to American chestnut restoration in the northeastern United States. *Restoration ecology* 19:55-63. <https://doi.org/10.1111/j.1526-100X.2009.00544.x>
- Huang H, Dane F, Kubisiak T (1998) Allozyme and RAPD analysis of the genetic diversity and geographic variation in wild populations of the American chestnut (Fagaceae). *American Journal of Botany* 85:1013–1013. <https://doi.org/10.2307/2446368>
- Hebard FV (2006) The backcross breeding program of the American chestnut foundation. *Journal of the American Chestnut Foundation* 19:55-77
- Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. *Trends in Ecology & Evolution* 24:599–605. <https://doi.org/10.1016/j.tree.2009.05.012>
- Hoegh-Guldberg O, Hughes L, McIntyre S, et al (2008) Assisted Colonization and Rapid Climate Change. *Science* 321:345–346. <https://doi.org/10.1126/science.1157897>

- Hutchinson GE (1957) Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology 22:415-457.
- IPCC (2014) Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. Core writing team, Pachauri RK, Meyer LA (eds). IPCC, Geneva, Switzerland
- IUCN (2013) Guidelines for reintroductions and other conservation translocations, Version 1.0. IUCN Species Survival Commission, Gland, Switzerland
- Iverson L, Prasad A, Matthews S (2008) Modeling potential climate change impacts on the trees of the northeastern United States. Mitigation and Adaptation Strategies for Global Change 13:487–516. <https://doi.org/10.1007/s11027-007-9129-y>
- Jacobs DF (2007) Toward development of silvical strategies for forest restoration of American chestnut (*Castanea dentata*) using blight-resistant hybrids. Biological Conservation 137:497–506. <https://doi.org/10.1016/j.biocon.2007.03.013>
- Jacobs DF, Dalglish HJ, Nelson CD (2013) A conceptual framework for restoration of threatened plants: the effective model of American chestnut (*Castanea dentata*) reintroduction. New Phytologist 197:378–393. <https://doi.org/10.1111/nph.12020>
- Jacobs DF, Oliet JA, Aronson J, Bolte A, Bullock JM, Donoso PJ, Landhäusser SM, Madsen P, Peng S, Rey-Benayas JM, Weber JC (2015) Restoring forests: What constitutes success in the twenty-first century? New Forests 46:601–614. <https://doi.org/10.1007/s11056-015-9513-5>
- Johnson JA, Altwegg R, Evans DM, et al (2016) Is there a future for genome-editing technologies in conservation? Animal Conservation 19:97–101. <https://doi.org/10.1111/acv.12273>
- Jones TA, Monaco TA (2009) A role for assisted evolution in designing native plant materials for domesticated landscapes. Frontiers in Ecology and the Environment 7:541–547. <https://doi.org/10.1890/080028>
- Kramer-Schadt S, Niedballa J, Pilgrim JD, Schroder B, Lindenborn J, Reinfelder V, Stillfried M, Heckmann I, Scharf AK, Augeri DM, Cheyne SM, Hearn AJ, Ross J, Macdonald DW, Mathai J, Eaton J, Marshall AJ, Semiadi G, Rustam R, Bernard H, Alfred R, Samejima H, Duckworth JW, Breitenmoser-Wuersten C, Belant JL, Hofer H, Wilting A (2013) The importance of correcting for sampling bias in MaxEnt species distribution models. Diversity and Distributions 19:1366–1379. <https://doi.org/10.1111/ddi.12096>
- Kunkel KE, Stevens LE, Stevens SE, Sun L, Janssen E, Wuebbles D, Rennells J, DaGaetano A, Dobson JG (2013a) Regional climate trends and scenarios for the U.S. National Climate Assessment. Part 1. Climate of the northeast U.S. (NOAA Technical Report NESDIS 142-1). U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Washington, DC. https://www.nesdis.noaa.gov/sites/default/files/asset/document/NOAA_NESDIS_Tech_Report_142-1-Climate_of_the_Northeast_US.pdf
- Kunkel KE, Stevens LE, Stevens SE, Sun L, Janssen E, Wuebbles D, Konrad CE, Fuhrman CM, Keim B, Kruk MC, Billot A, Needham H, Shafer M, Dobson JG (2013b) Regional climate trends and scenarios for the U.S. National Climate Assessment. Part 2. Climate of the southeast U.S. (NOAA Technical Report NESDIS 142-2). U.S. Department of Commerce, National Oceanic and

Atmospheric Administration, Washington, DC.
https://www.nesdis.noaa.gov/sites/default/files/asset/document/NOAA_NESDIS_Tech_Report_142-2-Climate_of_the_Southeast_US.pdf

- Kubisiak TL, Roberds JH (2003) Genetic variation in natural populations of American chestnut. *Journal of the American Chestnut Foundation* 16:43-48
- Kumar S, Stohlgren TJ (2009) Maxent modeling for predicting suitable habitat for threatened and endangered tree *Canacomyrica monticola* in New Caledonia. *Journal of Ecology and the Natural Environment* 1:094–098. <http://www.academicjournals.org/journal/JENE/article-abstract/C1CDB822968>
- Laikre L, Schwartz MK, Waples RS, Ryman N (2010) Compromising genetic diversity in the wild: unmonitored large-scale release of plants and animals. *Trends in Ecology & Evolution* 25:520–529. <https://doi.org/10.1016/j.tree.2010.06.013>
- Little EL (1977) Atlas of United States trees, Volume 4, Minor Eastern hardwoods: Misc. Pub. 1342. U.S. Department of Agriculture, Washington, DC.
- Liu C, White M, Newell G (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography* 40:778–789. <https://doi.org/10.1111/jbi.12058>
- MacKey BG, Lindenmayer DB (2001) Towards a Hierarchical Framework for Modelling the Spatial Distribution of Animals. *Journal of Biogeography* 28:1147–1166. <https://doi.org/10.1046/j.1365-2699.2001.00626.x>
- Mainali KP, Warren DL, Dhileepan K, McConnachie A, Strathie L, Hassan G, Karki D, Shrestha BB, Parmesan C (2015) Projecting future expansion of invasive species: comparing and improving methodologies for species distribution modeling. *Global Change Biology* 21:4464–4480. <https://doi.org/10.1111/gcb.13038>
- McKay JW (1942) Self-sterility in the Chinese chestnut (*Castanea mollissima*). *Proceedings of the American Society of Horticultural Science* 41:156–160.
- McKenney DW, Pedlar JH, Lawrence K, Campbell K, Hutchinson MF (2007) Potential impacts of climate change on the distribution of North American trees. *AIBS Bulletin* 57:939-948. <https://doi.org/10.1641/B571106>
- Merkle SA, Andrade GM, Nairn CJ, Powell WA, Maynard CA (2007) Restoration of threatened species: a noble cause for transgenic trees. *Tree Genetics & Genomes* 3:111–118. <https://doi.org/10.1007/s11295-006-0050-4>
- Merilä J, Hendry AP (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evolutionary Applications* 7:1–14. <https://doi.org/10.1111/eva.12137>
- Merow C, Smith MJ, Silander JA (2013) A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36:1058–1069. <https://doi.org/10.1111/j.1600-0587.2013.07872.x>

- Muir WM, Howard RD (2004) Characterization of environmental risk of genetically engineered (GE) organisms and their potential to control exotic invasive species. *Aquatic Sciences* 66:414–420. <https://doi.org/10.1007/s00027-004-0721-x>
- Newhouse AE, Polin-McGuigan LD, Baier KA, Valletta KE, Rottmann WH, Tschaplinski TJ, Maynard CA, Powell WA (2014) Transgenic American chestnuts show enhanced blight resistance and transmit the trait to T1 progeny. *Plant Science* 228:88–97. <https://doi.org/10.1016/j.plantsci.2014.04.004>
- Novak BJ, Maloney T, Phelan R (2018) Advancing a New Toolkit for Conservation: From Science to Policy. *The CRISPR Journal* 1:11-15. <https://doi.org/10.1089/crispr.2017.0019>
- Osborne PE, Seddon PJ (2012) Selecting suitable habitats for reintroductions: variation, change and the role of species distribution modeling. In Ewen JG, Armstrong DP, Parker KA, Seddon PJ (eds) *Reintroduction Biology: Integrating Science and Management*. Wiley-Blackwell, New York, pp. 73–104
- Paillet FL (2002) Chestnut: history and ecology of a transformed species. *Journal of Biogeography* 29:1517–1530. <https://doi.org/10.1046/j.1365-2699.2002.00767.x>
- Parker GG, Hill SM, Kuehnel LA (1993) Decline of understory American chestnut (*Castanea dentata*) in a southern Appalachian forest. *Canadian Journal of Forest Research* 23:259–265. <https://doi.org/10.1139/x93-035>
- Pearce J, Lindenmayer D (1998) Bioclimatic analysis to enhance reintroduction biology of the endangered helmeted honeyeater (*Lichenostomus melanops cassidix*) in southeastern Australia. *Restoration Ecology* 6:238-243. <https://doi.org/10.1046/j.1526-100X.1998.00636.x>
- Pearson R, Dawson T (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography* 12:361–371. <https://doi.org/10.1046/j.1466-822X.2003.00042.x>
- Pearson RG, Stanton JC, Shoemaker KT, Aiello-Lammens ME, Ersts PJ, Horning N, Fordham DA, Raxworthy CJ, Ryu HY, McNees J, Akçakaya HR (2014) Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change* 4:217-221. <https://doi.org/10.1038/nclimate2113>
- Peers MJL, Thornton DH, Majchrzak YN, et al (2016) De-extinction potential under climate change: extensive mismatch between historic and future habitat suitability for three candidate birds. *Biological Conservation* 197:164–170. <https://doi.org/10.1016/j.biocon.2016.03.003>
- Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259. <https://doi.org/10.1016/j.ecolmodel.2005.03.026>
- Potter KM, Hargrove WW, Koch FH (2010) Predicting climate change extirpation risk for central and southern Appalachian forest tree species. In: Rentch JS, Schuler TM (eds) *Proceedings from the Conference on the ecology and management of high-elevation forests in the central and southern Appalachian Mountains*. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA, pp 179-189

- Ramirez J, Jarvis A (2008) High resolution statistically downscaled future climate surfaces. International Center for Tropical Agriculture (CIAT); CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS), Cali, Colombia. <http://ccafs-climate.org/>
- Redford KH, Amato G, Baillie J, Beldomenico P, Bennett EL, Clum N, Cook R, Fonseca G, Hedges S, Launay F, Lieberman S, Mace GM, Murayama A, Putnam A, Robinson JG, Rosenbaum H, Sanderson EW, Stuart SN, Thomas P, Thorbjarnarson J (2011) What does it mean to successfully conserve a (vertebrate) species? *BioScience* 61:39–48. <https://doi.org/10.1525/bio.2011.61.1.9>
- Rhoades CC, Brosi SL, Dattilo AJ, Vincelli P (2003) Effect of soil compaction and moisture on incidence of phytophthora root rot on American chestnut (*Castanea dentata*) seedlings. *Forest Ecology and Management* 184:47–54. [https://doi.org/10.1016/S0378-1127\(03\)00147-6](https://doi.org/10.1016/S0378-1127(03)00147-6)
- Robert A, Thévenin C, Princé K, et al (2016) De-extinction and evolution. *Functional Ecology* 31:1021-1031. <https://doi.org/10.1111/1365-2435.12723>
- Rodriguez JP (2007) The Application of Predictive Modelling of Species Distribution to Biodiversity Conservation. *Diversity and Distributions* 13:243–251. <https://doi.org/10.1111/j.1472-4642.2007.00356.x>
- Rödger D, Kielgast J, Bielby J, Schmidlein S, Bosch J, Garner TWJ, Veith M, Walker S, Fisher MC, Lötters S (2009) Global amphibian extinction risk assessment for the panzootic chytrid fungus. *Diversity* 1:52–66. <https://doi.org/10.3390/d1010052>
- Rovzar C, Gillespie TW, Kawelo K (2016) Landscape to site variations in species distribution models for endangered plants. *Forest Ecology and Management* 369:20–28. <https://doi.org/10.1016/j.foreco.2016.03.030>
- Russell EWB (1987) Pre-Blight distribution of *Castanea dentata* (Marsh.) Borkh. *Bulletin of the Torrey Botanical Club* 114:183-190. <https://doi.org/10.2307/2996129>
- Rutkow E (2012) *American canopy: Trees, forests, and the making of a nation*. Simon and Schuster, New York
- Saielli TM, Schaberg PG, Hawley GJ, Halman JM, Gurney KM (2012) Nut cold hardiness as a factor influencing the restoration of American chestnut in northern latitudes and high elevations. *Canadian Journal of Forest Research* 42:849–857. <https://doi.org/10.1139/x2012-033>
- Santoro J (2013) American chestnut (*Castanea dentata*) habitat modeling: identifying suitable sites for restoration in Shenandoah National Park, Virginia. Master's thesis, Duke University
- Schaberg P, Murakami P, Hawley G, Collins K (2017) American chestnut restoration in New England - cold damage as an added challenge. *New England Society of American Foresters News Quarterly* 78: 8-11.
- Schlaepfer MA, Runge MC, Sherman PW (2002) Ecological and evolutionary traps. *Trends in Ecology & Evolution* 17:474–480. [https://doi.org/10.1016/S0169-5347\(02\)02580-6](https://doi.org/10.1016/S0169-5347(02)02580-6)
- Schlaepfer MA, Sherman PW, Blossey B, Runge MC (2005) Introduced species as evolutionary traps. *Ecology Letters* 8:241–246. <https://doi.org/10.1111/j.1461-0248.2005.00730.x>

- Schwartz MW (2012) Using niche models with climate projections to inform conservation management decisions. *Biological Conservation* 155:149-156. <https://doi.org/10.1016/j.biocon.2012.06.011>
- Searcy CA, Shaffer HB (2016) Do ecological niche models accurately identify climatic determinants of species ranges? *The American Naturalist* 187:423–435. <https://doi.org/10.1086/685387>
- Seddon PJ (2010) From reintroduction to assisted colonization: moving along the conservation translocation spectrum. *Restoration Ecology* 18:796–802. <https://doi.org/10.1111/j.1526-100X.2010.00724.x>
- Seddon PJ, Griffiths CJ, Soorae PS, Armstrong DP (2014) Reversing defaunation: Restoring species in a changing world. *Science* 345:406–412. <https://doi.org/10.1126/science.1251818>
- Skousen J, Cook T, Wilson-Kokes L, Pena-Yewtukhiw E (2013) Survival and growth of chestnut backcross seeds and seedlings on surface mines. *Journal of Environment Quality* 42:690-695. <https://doi.org/10.2134/jeq2012.0368>
- Steiner, KC (2006) Regional adaptation in American chestnut. In: Steiner KC, Carlson JE (eds) *Restoration of American chestnut to forest lands: Proceedings of a conference and workshop*. National Park Service, Washington, DC, pp 123-126
- Steiner KC, Westbrook JW, Hebard FV, Georgi LL, Powell WA, Fitzsimmons SF (2016) Rescue of American chestnut with extraspecific genes following its destruction by a naturalized pathogen. *New Forests* 48:317-336. <https://doi.org/10.1007/s11056-016-9561-5>
- Stephenson SL, Adams HS, Lipford ML (1991) The present distribution of chestnut in the upland forest communities of Virginia. *Bulletin of the Torrey Botanical Club* 118:24-32. <https://doi.org/10.2307/2996972>
- Stilwell KL, Wilbur HM, Werth CR, Taylor DR (2003) Heterozygote Advantage in the American Chestnut, *Castanea dentata* (Fagaceae). *American Journal of Botany* 90:207–213. <https://doi.org/10.3732/ajb.90.2.207>
- Stockwell CA, Hendry AP, Kinnison MT (2003) Contemporary evolution meets conservation biology. *Trends in Ecology & Evolution* 18:94–101. [https://doi.org/10.1016/S0169-5347\(02\)00044-7](https://doi.org/10.1016/S0169-5347(02)00044-7)
- The American Chestnut Foundation (TACF) (2018) Regional breeding. <https://www.acf.org/our-work/regional-breeding/> Accessed 24 March 2018
- Thomas MA, Roemer GW, Donlan CJ, et al (2013) Gene tweaking for conservation. *Nature* 501:485–486. <https://doi.org/10.1038/501485a>
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC., Erasmus BF, De Siqueira MF, Grainger A, Hannah L, Hughes L (2004) Extinction risk from climate change. *Nature* 427:145-148. <https://doi.org/10.1038/nature02121>
- Tiedje JM, Colwell RK, Grossman YL, et al (1989) The planned introduction of genetically engineered organisms: ecological considerations and recommendations. *Ecology* 70:298–315. <https://doi.org/10.2307/1937535>

- Vandermast DB, Van Lear DH (2002) Riparian vegetation in the southern Appalachian mountains (USA) following chestnut blight. *Forest Ecology and Management* 155:97–106.
[https://doi.org/10.1016/S0378-1127\(01\)00550-3](https://doi.org/10.1016/S0378-1127(01)00550-3)
- van Oppen MJH, Puill-Stephan E, Lundgren P, De'ath G, Bay LK (2014) First-generation fitness consequences of interpopulational hybridisation in a Great Barrier Reef coral and its implications for assisted migration management. *Coral Reefs* 33:607–611. <https://doi.org/10.1007/s00338-014-1145-2>
- van Oppen MJH, Oliver JK, Putnam HM, Gates RD (2015) Building coral reef resilience through assisted evolution. *Proceedings of the National Academy of Sciences* 112:2307–2313.
<https://doi.org/10.1073/pnas.1422301112>
- Vitt P, Havens K, Kramer AT, Sollenberger D, Yates E (2010) Assisted migration of plants: Changes in latitudes, changes in attitudes. *Biological Conservation* 143:18–27.
<https://doi.org/10.1016/j.biocon.2009.08.015>
- Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology, Evolution, and Systematics* 36:519–539.
<https://doi.org/10.1146/annurev.ecolsys.36.102803.095431>
- Willis KJ, Birks HJB (2006) What Is Natural? The need for a long-term perspective in biodiversity conservation. *Science* 314:1261–1265. <https://doi.org/10.1126/science.1122667>
- Wisz MS, Hijmans RJ, Li J, Peterson AT, Graham CH, Guisan A (2008) Effects of sample size on the performance of species distribution models. *Diversity and distributions* 14:763–773.
<https://doi.org/10.1111/j.1472-4642.2008.00482.x>
- Woodward FI, Williams BG (1987) Climate and plant distribution at global and local scales. *Vegetatio* 69:189–197. <https://doi.org/10.1007/BF00038700>
- Woodward FI (1990) The impact of low temperatures in controlling the geographical distribution of plants. *Philosophical Transactions of the Royal Society of London B* 326:585–93.
<https://doi.org/10.1098/rstb.1990.0033>
- Wyborn C, van Kerkhoff L, Dunlop M, et al (2016) Future oriented conservation: knowledge governance, uncertainty and learning. *Biodiversity and Conservation* 25:1401–1408.
<https://doi.org/10.1007/s10531-016-1130-x>
- Yackulic CB, Chandler R, Zipkin EF, Royle JA, Nichols JD, Campbell Grant EH, Veran S (2013) Presence-only modelling using MAXENT: when can we trust the inferences? *Methods in Ecology and Evolution* 4:236–243. <https://doi.org/10.1111/2041-210x.12004>
- Yang X-Q, Kushwaha SPS, Saran S, Xu J, Roy PS (2013) Maxent modeling for predicting the potential distribution of medicinal plant, *Justicia adhatoda* L. in Lesser Himalayan foothills. *Ecological Engineering* 51:83–87. <https://doi.org/10.1016/j.ecoleng.2012.12.004>
- Zhebentyayeva T, Chandra A, Abbott AG, Staton ME, Olukolu BA, Hebard FV, Georgi LL, Jeffers SN, Sisco PH, James JB, Nelson CD (2014) Genetic and genomic resources for mapping resistance to *Phytophthora cinnamomi* in chestnut. *Acta Horticulturae* 1019:263–270.
<https://doi.org/10.17660/ActaHortic.2014.1019.40>

CHAPTER 3

RESTORATION AND RESISTANCE: POLANYI'S DOUBLE MOVEMENT AND THE POLITICS OF GENETIC TECHNOLOGICAL SCIENCE

Abstract

Innovations in genetics and genomics have drawn attention from critical scholars in geography, science and technology studies (STS), sociology, and anthropology as technologies that enable the enactment and extension of neoliberal capitalism, particularly in agriculture. Many of these critiques are related to the tendency of genetic science to promote reductionism in the way we understand and interact with other organisms, including the notion that they can be simply reprogrammed through genetic modification. In agriculture, this reductionist perspective has ignored the complexity of natural systems and facilitated the privatization and commodification of plant genetic resources through patents and other intellectual property protections. But many of these patterns were described well before the use of genetic technologies in biodiversity conservation became an anticipated possibility. This new application of genetic technological science, examined here through the case of American chestnut restoration, embodies important discontinuities with neoliberal critiques of genetic technologies in agriculture. Using the theoretical lenses of Karl Polanyi's double movement and Langdon Winner's description of technological politics, this paper explains why and how social and biological systems have presented some resistance to the neoliberalization of nature. Drawing on participant observation, interviews, and historical analysis, we specifically describe how the anticipations, agency, and normative commitments of the developers of this technology, combined with the biology of American chestnut and the context of restoration, have resisted the genetic commodification of nature.

Introduction

In an unassuming building on the campus of the State University of New York, College of Environmental Science and Forestry (SUNY-ESF), faculty, students, and postdoctoral researchers affiliated with the American Chestnut Research and Restoration Project are engaged in an effort unlike any other. Since 1989, the project has been using the tools of genetic engineering to develop American chestnut (*Castanea dentata*) trees that are resistant to *Cryphonectria parasitica*, or chestnut blight, an introduced fungal pathogen that brought the species to functional extinction in the early 1900s. Although the notion of a biotechnology lab may conjure images of sterility and security, the project is surprisingly low-key. William Powell, the project's Co-Director, sits in an office crowded with houseplants and papers, grading genetics exams and responding to emails from regulators, skeptics, and supporters of forest biotechnology. Down the hall, his graduate students transform American chestnut embryos, adding a gene from wheat that allows them to tolerate blight infection; they also occasionally oversee ecological experiments in the basement. In the next building, a postdoc coaxes clones from transformed embryos, then bathes them in hormone cocktails intended to replicate the developmental signals typically received inside a protective chestnut shell. Outside, in the greenhouse, an undergraduate waters and fertilizes rows of potted seedlings developed from tissue culture; colorful, fuzzy pipe cleaners hold the developing plants to their stakes, training them to grow straight and tall. A short drive across town, these transgenic trees finally meet sun and earth in one of the project's gated, but modest field sites. Most of these trees will be cut down to stumps -- or coppiced -- before they are a few years old, and all of them will be bagged before producing pollen. Powell and his colleagues hope that after federal regulatory approval, their trees will be ready for large-scale distribution. Although trees produced by the program may eventually be sold to offset production costs, their genetic material will not be patented. These trees are for unrestricted and open release for the restoration of American chestnut to forests across the species' historical range.

Transgenic American chestnut trees are just one of many genetics- and genomics-based strategies that have been attempted in the protection and restoration of this heritage forest species. Researchers have also used genetic engineering to transform the chestnut blight fungus (Anagnostakis et al., 1989) and to

insert genes from plants other than wheat into the American chestnut genome (FHI, 2018). Genetic maps have been produced for Chinese, European, and hybrid American/Chinese chestnut trees in order to understand the genetic basis of blight-resistance in the chestnut species that have evolved it (Kubisiak et al., 1997; Sisco et al., 2004). Additionally, the development of a genetic map for American chestnut and methods for identifying blight-resistance using DNA markers rather than cankers, the tell-tale signal of blight infection, are currently planned (Steiner et al., 2017).

Innovations in genetics and genomics like those being used in American chestnut restoration have drawn attention from critical scholars across the social sciences and humanities as technologies that have enabled the enactment and extension of neoliberal capitalism, particularly in agriculture (Busch, 2010; McAfee, 2003; Pechlaner and Otero, 2008; Schurman and Munro, 2010). Employing neoliberalism, by and large, as a strongly negative term, these and other scholars have linked genetic technologies to scientific and political processes that privilege corporations (Kloppenburg, 2005), threaten small-scale and subsistence production and associated livelihoods (Otero and Pechlaner, 2008), and irrevocably alter environmental systems by ignoring their complexity (McAfee, 2003). However, many of the patterns attributed to genetic science and its technologies were described well before their use in biodiversity conservation became an anticipated possibility. Their use in American chestnut restoration -- by non-profit organizations, for the manipulation of a wild, threatened species, and with unconventional intellectual property protections -- is positioned to disrupt philosophies and precedents in plant biotechnology, including prevailing assumptions about genetic technologies as inherently complicit in the neoliberal project. While this case may herald a changing political economy in plant biotechnology (Harrison et al., 2017), we suggest that it is the specific context of species restoration that has freed genetic technoscience from some of the market logics that have characterized its use in agriculture.

The purpose of this paper is to make sense of these apparent inconsistencies by combining theoretical insights on the uneven politics of technological artifacts from science and technology studies (STS) and the uneven nature of neoliberalism from geography, particularly political ecology. Himley (2008: 445) has suggested that the growing body of scholarship on neoliberal environmental governance

within the field of geography “would profit from more robust ethnographic accounts of the complex and place-based sets of practices through which particular actors have produced, reproduced, and challenged these novel modes of governance – or, alternatively, have failed to do so.” This paper reflects that kind of attention to the geographically contingent and complex ways in which situated actors have both reproduced and challenged neoliberal patterns. In what follows, we first relate a technological history of American chestnut restoration, culminating in contemporary efforts to reintroduce the species principally using genomics-informed breeding and genetic engineering. Then, we briefly review the concept of neoliberalism and critiques that frame genetic technologies in agriculture as neoliberal. Drawing on three years of ethnographic data, we then describe the ways in which the use of genetic technologies in American chestnut restoration demonstrates important -- though admittedly incomplete -- discontinuities with the use of these technologies in agriculture. Based on Winner’s (1980) explanation of the theory of technological politics, we suggest that rather than being *necessarily* neoliberal, genetic technologies are highly compatible with the neoliberal project in some contexts. Finally, we employ Polanyi’s (1944) theory of the double movement to explain *why* American chestnut restoration presents substantial challenges to the privatization, commodification, and commercialization of nature using genetic technologies.

A technological history of American chestnut conservation

Likely imported along with shipments of Asian chestnut trees in the late 1800s, chestnut blight was first detected on American chestnut trees growing in what is now the Bronx Zoo in 1904 (Freinkel, 2007). In the following years, heated debates would take place over both the identity of the pathogen and the appropriate approach to its control (Freinkel, 2007). The earliest attempts to treat chestnut blight infection were chemical and physical, focused on the use of fungicides, tree surgery to remove infected limbs, and the removal of entire infected trees from cultivated and forest stands (Curry, 2014; Freinkel, 2007). Quarantine measures were also implemented, eventually supported by the passage of the Plant Quarantine Act, which aimed to limit the importation of additional potential plant pathogens in light of

the destruction wrought by chestnut blight (Freinkel, 2007). These measures were largely unsuccessful. Anthropogenic interaction with American chestnut over centuries had created nearly pure stands of the tree in some regions of its expansive range, to the extent that it was said a squirrel could travel from Georgia to Maine without touching anything but American chestnut canopy (Freinkel, 2007). This host density and distribution also allowed chestnut blight to spread rapidly and reproduce prolifically, while a lack of native tolerance or resistance to the blight resulted in infection and die-off in nearly every American chestnut tree in its wake.

Failure to kill or limit the spread of chestnut blight quickly turned attention and effort to the possibility of inducing blight-resistance in American chestnut trees (Curry, 2014). In 1914, a botanist named Arthur Graves suggested that the only way to save the species might be to “outwit” the blight fungus by breeding American chestnut with its blight-resistant Asian cousins, a strategy that was used widely in corn breeding (Freinkel, 2007). Not until 1931, after becoming a curator at the Brooklyn Botanic Garden, did Graves finally start work on a breeding program for American chestnut (Freinkel, 2007). In the meantime, however, scientists at the United States Department of Agriculture (USDA) had begun an intensive effort to cross American chestnut with *Castanea mollissima*, the Chinese chestnut, with the hope of producing trees with the blight-resistance of the Chinese species and the form and function of the American species (Curry, 2014; Freinkel, 2007; Jacobs et al., 2013). When the USDA’s hybridization effort ended in 1960, an estimated 10,000 distinct crosses had been made, but both Graves’ and the USDA’s program ended without a great deal of success; hybrid trees rarely maintained what were considered the essential characteristics of American chestnut, principally its height and growth form (Curry, 2014). The USDA program did, however, leave two important legacies. For one, the agency had encouraged foresters, landowners, sportsmen, and nurseries to plant imported Asian chestnut seeds as an ecological and culinary replacement for American chestnut, and these trees still populate yards and Appalachian forests (Freinkel, 2007). Additionally, later breeding programs would build upon the hybrid germplasm produced by USDA, as well as the lessons learned through its failure (Freinkel, 2007).

The breeding efforts at USDA began just after Gregor Mendel's experiments in heredity were rediscovered, and the relationships between plant genotypes and phenotypes were still being worked out (Freinkel, 2007). Consequently, those involved in the effort (including Norman Borlaug, who would eventually win a Nobel Prize for his work on hybrid agricultural crops) knew little about genetics at the time (Freinkel, 2007). Building on genetic knowledge established in the intervening years, in the 1980s, Charles Burnham, a retired corn geneticist, hypothesized that the backcross breeding approach that worked in agriculture could also work for American chestnut (Burnham, 1988). The non-profit American Chestnut Foundation (TACF) was established to try it, initiating a restoration program that continues today, guided by a mission to return American chestnut to its native range (TACF, 2018a). Following Burnham's prescription, for almost four decades, TACF has been crossing surviving American chestnut trees and blight-resistant Chinese chestnut trees; the hybrid progeny are then crossed back to the American parent in an attempt to transfer the blight-resistance of the Chinese species while maintaining or recovering the characteristics of the American species (Hebard, 2005). Hybrid trees in later generations of this program display levels of blight-resistance that are intermediate between American and Chinese resistance (Steiner et al., 2017). Members of state chapters of TACF are now crossing these trees, which are bred in Meadowview, Virginia, with surviving, pure American chestnut trees located in their respective regions in order to improve the local adaptation of the backcross population (Steiner et al., 2017). Meanwhile, the national organization continues to cull their breeding orchard in Meadowview, currently aiming to reduce 10,000 trees from the last backcross generation down to the 500 most resistant ones (Steiner et al., 2017). To aid in this process, scientists affiliated and collaborating with TACF are preparing to produce a reference map of the American chestnut genome and develop markers for genomic selection, an efficient, DNA-based method for detecting blight-resistance among their hybrid trees (Steiner et al., 2017).

In 1989, members of the New York Chapter of TACF approached Powell and a colleague, Charles Maynard, at SUNY-ESF with an interest in exploring the potential use of the emerging science of genetic engineering to produce blight-resistant trees; thus began the American Chestnut Research and

Restoration Project (Powell, 2014). After some failed attempts to use antimicrobial peptides to weaken the fungal cells of *C. parasitica*, struggling for years to grow American chestnut embryos under lab conditions, and then trying to design appropriate genetic constructs, in 2012, Powell's lab successfully developed transgenic American chestnut trees that tolerate blight infection (Powell, 2014; Zhang et al., 2013). Although a number of genes have been tested, an oxalate oxidase gene from wheat plants has been by far the most promising; this gene, which codes for an enzyme that neutralizes the destructive acid produced by *C. parasitica*, confers levels of blight-resistance that are equal to or higher than that of Asian chestnut species (Zhang et al., 2013). Two transgenic lines carrying this gene, named Darling 54 and Darling 58 (after Herb Darling, the founder of TACF's New York Chapter), are expected to undergo federal consideration for deregulation in the United States later this year, with an application for release in Canada to follow shortly thereafter (William Powell, personal communication, October 7, 2017). Until recently, TACF's national leadership maintained some distance from and ambiguity towards a biotechnological approach to blight-resistance; however, SUNY-ESF's transgenic trees were officially incorporated into TACF's latest Strategic Plan for restoration and are now expected to be used in conjunction with germplasm developed in the backcross breeding program (TACF, 2017).

At least one additional program has been integral to the development of genetic and genomic tools for American chestnut restoration. In 2009, with financial support from the U.S. Endowment for Forests and Communities, the USDA Forest Service, and Duke Energy, the Institute of Forest Biotechnology (later renamed the Institute of Forest Biosciences) established the Forest Health Initiative (FHI), a collaborative program that aimed to demonstrate the potential of emerging biotechnologies to address pressing problems in forest health (FHI, 2018). The FHI adopted American chestnut as its "test case" (FHI, 2018) and, in the interest of making rapid progress in the development and field testing of disease-resistant American chestnut trees, enrolled experts already working on American chestnut, including the team at SUNY-ESF and researchers affiliated with TACF. FHI projects have now ended, but they funded a number of developments that have dramatically increased the integration of genetic technologies into chestnut restoration, including assays for earlier detection of blight resistance in

transgenic plants (Newhouse et al., 2014), improved somatic embryogenesis techniques for generating whole plants from transformed cells (Holtz et al., 2016), a reference genome for Chinese chestnut (Fang et al., 2013; Kubisiak et al., 2013), and the transformation of American chestnut embryos with candidate blight-resistance genes from Chinese chestnut (FHI, 2018). FHI was intentionally ground-breaking in both its commitment to public interests and its “braided process” that considered regulatory, environmental, and social dimensions of the use of genetic technologies for forest health, concurrent with the development of scientific knowledge and protocols (FHI, 2018).

Technologies of neoliberal governance

Many of the technologies being adopted by groups involved in American chestnut restoration were first used in agriculture and in that context have been associated with neoliberal forms of governance. In general, as a *new (neo) liberalism*, neoliberalism refers to an approach to governance that expands upon earlier, *laissez-faire* economic policies in which markets were considered autonomous, directed only by the self-interested behavior of free individuals (Harvey, 2007) -- what Adam Smith called the invisible hand. Under liberal economic regimes, which dominated until the atrocities of Nazi Germany brought about World War II, the state remained central to the provision of many public services, including healthcare, education, and environmental management (Harvey, 2007). In direct response to the abuses of communism and the inefficiencies of the welfare states that followed, proponents of *neoliberalism* promoted economic freedom -- and a resurgence of liberal economic policies -- as the means to political freedom (Friedman, 2009). Committed to the notion that market competition is the most efficient, rational, and fair way to distribute goods, services, and information, neoliberalism seeks to limit the state’s role to the creation and maintenance of the conditions required for free markets and to extend market logics into new realms (Harvey, 2007). This resurrection and reshaping of liberal capitalism furthered the transformation of human labor, natural resources, and money and credit into commodities that could be bought and sold on a market; Polanyi (1944) called these “fictitious commodities” because they were not originally amenable to being sold, nor were they developed for that

purpose (Block, 2001). Thus, although principally an economic project on the surface, neoliberal reforms have been accompanied by broader and more fundamental changes in the relationships between states, publics, markets, and nature (Castree, 2010). In this vein, Michel Foucault (2008: 218) described neoliberalism as a new “art of government” or “governmentality” -- “a whole way of thinking and being” that shapes all dimensions of human existence from the economy to reproduction. Today, “neoliberalism is very much a critic’s term” (Castree, 2010: 1726), employed largely by scholars concerned with the commodification of human and non-human bodies and the roll-back of government protections for the poor.

As a sociologist focused on mechanisms of governance in agricultural systems, Busch (2010) has suggested that neoliberalism might be best understood as a combination of social technologies -- including organizations, institutions, and strategies -- and artifacts -- various physical and digital technologies -- that have been particularly influential in and compatible with the extension of markets into new arenas. Genetic and genomic technologies are implicated among these “technologies of neoliberal governance” principally because they have facilitated the private enclosure and commodification of nature, especially genetic resources (Busch, 2010). Privatization has broadly entailed the application of ownership rights to resources that were once public or unowned. Throughout the 20th century, intellectual property protections, particularly patents, were fundamental to this process. Patent laws have explicitly and formally excluded the products of nature, but what counts as natural product has been unclear and contested for over a century, especially in light of genetic science and technologies, which have been used to expand patent protection to both organisms and genetic sequences (Beauchamp, 2013). Genetic science has likewise aided the commodification of nature, or its transformation into tradable goods and treatment as a source of capital. For example, in agriculture, genetic engineering dramatically reduced the time and space required for moving genetic material between organisms and thus increased the rate at which new plant varieties could be moved to market (Busch, 2010). Both privatization and commodification have received a boon from the notion that genes are discrete, transferrable, predictable, and deterministic in their influence on the phenotypes of living organisms -- what McAfee (2003) refers to as “molecular-

genetic reductionism.” Critics argue that this kind of reductionism has drawn attention away from both the root causes of agricultural problems and alternative approaches to their resolution that are situated at levels other than the molecular (Busch, 2010; McAfee, 2003).

Importantly, genetic technologies embody practices of knowledge production as well as the production of artifacts, and science itself has also been a location for critical analysis of the influence of neoliberalism. After all, “[t]he fundamental role of the market is not, according to neoliberalism, the mere exchange of things, but rather the processing and conveyance of knowledge or information” (Lave et al., 2010: 662). STS scholars have employed the term *technoscience* -- first used by philosophers to refer to science that both emerges from and produces technological artifacts -- to describe the ways in which science is tied to and co-produced with its technological and social context (Latour, 1987; Haraway, 1990). Understanding that technoscience shapes the enactment of neoliberalism and is in turn shaped by it, Lave et al. (2010) have called for more careful attention to the influence of neoliberalism on the structure and content of science, in addition to its products or artifacts. Distilling scholarship from a wide range of fields, they suggest that, in general, neoliberalism has resulted in the commercialization of university science -- or its orientation towards profit, rather than public good -- through a number of processes. These include the expansion of intellectual property protections and the commodification of knowledge; a reduction in public funding for science that requires universities to act like corporations; reliance on market forces to decide intellectual disputes; and an increasing focus in public research on the development of knowledge and products with profit potential (Lave et al., 2010). Neoliberal reforms initiated in the U.S. in the 1980s both encouraged private investment in biotechnology and allowed publicly-funded research to be patented (Cooper, 2008), creating laboratories that operated like businesses (Kleinman, 1998; Kleinman & Vallas, 2006; Krimsky, 1991). Additionally, as universities increasingly rely on alternative sources of funding, including public-private partnerships (Evans, 2010), they become more beholden to the commercial logics of their funders. As one example in agricultural science, this shift has resulted in the disproportionate production of hybrid and genetically engineered crops that benefit

industrial farming systems typical in the global North but are incongruous with subsistence systems common in the global South (Glover, 2010; Brooks, 2015).

Is genetic technoscience inherently neoliberal?

This paper emerged from initial observations that the use of genetic technologies in efforts to develop blight-resistant American chestnut trees appears to disrupt some of the patterns generally described for genetic technoscience in other, particularly agricultural, contexts. As Hoeyer (2007a; 2007b) found in exchange systems for human biological materials, we noted that prevailing assumptions about the smooth expansion of market logics to fictitious commodities were incompatible with observed social and biological resistance to that process. Hoeyer (2007b) insists that, in his case, simply interpreting the transfer of human blood and tissues for transplantation or experimentation as a form of commodification requires either ignoring the agency and concern of those involved or claiming their involvement in a conspiracy and deceit about their true intentions. Instead, he argues for taking concerns about the “transgression of the boundary between person and commodity at its face value” and examining how those concerns shaped the policies and practices that emerged to govern the exchange of human biological materials (Hoeyer, 2007b: 332). We likewise found conclusions about the political economy of genetic technoscience to be at odds with our observations of its application to American chestnut, and thus sought to both explore and explain this apparent paradox, while taking seriously the sentiments of the actors involved rather than assuming intent, particularly malicious intent.

The theory of technological politics (Winner, 1980) provides theoretical grounding for reconsidering the politics of genetic technoscience in light of its use in American chestnut restoration. Challenging the notion that social change is driven by technological innovation and the idea that the conformation and consequences of technologies are wholly determined by their social context, the theory of technological politics draws attention back to the fundamental characteristics of technological artifacts as the starting place for considering the kinds of political possibilities associated with their use (Winner, 1980). Even for technologies that are consistently accompanied by particular political or economic structures, “[t]he important question is: Does this state of affairs derive from an unavoidable social

response to intractable properties in the things themselves, or is it instead a pattern imposed independently by a governing body, ruling class, or some other social or cultural institution to further its own purposes?” (Winner, 1980: 131). Drawing from a set of diverse case studies, Winner (1980) ultimately demonstrated that technologies can be political in two different ways: 1) because they are necessarily or strongly aligned with certain political structures; in other words, they are inherently political, or 2) because they are *used* politically, often as a way to settle social issues; they are not inherently political, but may still have political consequences that become embodied in ways that outlast initial motivations for the technology. In much of the existing literature on genetic technoscience in agricultural contexts, genetic technologies have been discussed as inherently political, having properties that inevitably enroll them in the realization of neoliberal goals. However, new applications of genetic and genomic science in biodiversity conservation prompt us to re-examine the assumption that this association with neoliberal outcomes is unavoidable. In fact, in noting that technologies of neoliberal governance should not be, by default, unacceptable to the critics of neoliberalism, even Busch (2010) seems to leave room for genetics and genomics to realize other political possibilities.

In the following section, we draw on three years of in-depth and mixed-method ethnographic research to describe the ways in which previous conclusions about the neoliberal disposition of genetic technoscience are complicated by its application to American chestnut restoration. This work began with document analysis and literature review of materials published by groups involved in various dimensions of American chestnut restoration. Participant observation was also conducted at three annual meetings of TACF, as well as at an annual U.S. EPA - Region 2 Indian Nation Leaders Meeting, at which the transgenic American chestnut was discussed by Powell and others. We also visited American chestnut breeding orchards and restoration locations in Meadowview, VA and Portland, ME and laboratories and transgenic field sites in Syracuse, NY. Additionally, ten qualitative, semi-structured interviews were conducted in-person and by phone in 2017 with scientists involved in American chestnut restoration. Interview participants were purposively selected among the relatively small staff (fewer than 20 people each) and Board of TACF and scientists affiliated with the American Chestnut Research and Restoration

Project at SUNY-ESF. Below, we consider the ways in which American chestnut resists or reifies three neoliberal patterns consistently discussed by critical scholars: the privatization of genetic resources and knowledge, the transformation of nature into a tradable commodity, and the orientation of genetic technoscience towards commercial practices and priorities.

The political economy of genetic technoscience in American chestnut restoration

Privatization

One of the most glaring inconsistencies between neoliberal patterns of privatization in agricultural biotechnology and the application of genetic engineering to American chestnut restoration is the lack of intellectual property (IP) protection sought for the transgenic trees being developed by the American Chestnut Research and Restoration Project at SUNY-ESF. Powell has explained that the decision to forgo a patent on their transgenic lines was motivated primarily by early realization that doing so would be an impediment to the plan for eventual chestnut restoration. In direct opposition to Powell's goals, a patent would constrain the spread of the oxalate oxidase transgene into American chestnut populations by limiting the ability of conservationists and members of the public to freely plant transgenic trees and cross them with surviving American chestnut trees or hybrids produced through TACF's backcross program. A number of scientists affiliated with TACF, who consider Powell's lack of proprietary interest to be "noble," suggested in interviews that his decision might also be linked to the collaborative nature of American chestnut restoration. The research conducted at SUNY-ESF and the transgenic trees that have resulted from that research have been enabled by a wide variety of funding sources; in particular, the financial backing and political clout of TACF members, especially those of the New York Chapter, have been paramount to the success of the project. Although Powell originally received some pressure from SUNY-ESF to patent his trees (William Powell, personal communication, October 7, 2017), his refusal to do so may thus also reflect resistance to the prospect of the university singularly benefitting from what has been a concerted effort.

Lave et al. (2010: 666) insist that a focus on patents has distracted critical attention away from other locations of IP fortification, especially material transfer agreements, which have “become the instrument of choice to control the commercial implications of cutting-edge research,” especially when the marketability of future developments made with those materials remain uncertain. TACF maintains IP protection on germplasm generated in their breeding program through a Germplasm Agreement, which is signed by all collaborators who receive plant materials from the organization, including Powell (TACF, 2018b; William Powell, personal communication, October 7, 2017). TACF relies on volunteers working in locations across the native range of American chestnut to test the fitness of backcross populations for varied environmental conditions, to develop locally-adapted germplasm, and to investigate the silvicultural practices required for reintroducing American chestnut in forests and other landscapes, such as mined lands. To this end, the organization distributes plant materials produced through the backcross program in Meadowview, aware that these materials contain varying levels of blight-resistance and are inconsistent in other traits as well. The Germplasm Agreement prohibits the propagation of materials from early backcross generations and the sale or transfer of any American chestnut germplasm received from TACF without the organization’s approval because:

(1) the Recipient and TACF wish to preserve TACF’s rights to such genetic material; and (2) the Recipient and TACF most emphatically do not want any person to take such material and market it, or to market any progeny from it; the material may not have the characteristics desired or have characteristics that are not consistent with the goal of TACF, namely “the Restoration of the American Chestnut”, and not a Chinese or other type of tree; and (3) the Recipient and TACF do not want to be identified with the distribution, increase or marketing of material that has the potential of diluting the resident American chestnut population in the Appalachian mountains.

(TACF, 2018b)

While Powell sees foregoing patent protection as important for facilitating restoration, TACF “most emphatically” views maintaining IP as necessary for successful restoration. In pursuit of its goal to restore populations of *American* chestnut to the species’ native range, the organization is interested in keeping

germplasm that retains too many characteristics of Chinese chestnut or is otherwise unfit for forest restoration out of open circulation. However, this agreement also clearly maintains TACF's options for commercialization. Ten years ago, Jacobs (2007: 504) reported that TACF "expects to develop cultivar names with trademark protections for deployment of blight-resistant germplasm," but our recent interviews with TACF staff and Board members reveal continuing uncertainty within the Foundation about the future ownership, large-scale production, and distribution of blight-resistant, backcross trees.

In addition to protections on TACF's technological artifacts -- its hybrid germplasm -- the organization's Germplasm Agreement also protects the knowledge generated from research on its plant materials: the agreement "conveys only a right to carry out research, evaluations and/or field testing on the germplasm *on behalf of and in consultation with TACF*" (TACF, 2018b; italics added). However, contrary to what Evans (2010) found to be true for public-private partnerships in plant breeding, this language does not appear to limit the ability of university researchers to present on or publish research findings related to the molecular characterization or ecological performance of TACF's backcross trees. As a non-profit with a small staff, TACF relies on these collaborations for technical expertise and experimental resources, and university scientists publish their findings independently. The structure and guiding principles of the Forest Health Initiative's (FHI) work on American chestnut are also inconsistent with the privatization of knowledge. The research conducted by the FHI committees -- the Science Advisory Committee, the Social and Environmental Committee, and the Policy and Regulatory Committee -- was explicitly imagined as a public good and "was predicated on the core operating values of the FHI including that the public owns the intellectual property created by FHI-sponsored research" (FHI, 2018). All knowledge produced through research funded by FHI is thus made publicly available online. This lack of privatization may be at least partly attributable to FHI's financial structure, reliant as it was on funds from the USDA Forest Service, which requires science produced by its staff and beneficiaries to be open-access and in the public domain.

Commodification

Consistent with the use of genetic technologies in agriculture, ongoing efforts to use genetic engineering and genomic sequencing in American chestnut restoration were initiated in the interest of producing more blight-resistant trees in less time with less labor (Powell, 2014; FHI, 20107; TACF, 2017). As Busch et al. (1991) describe for genetic technoscience in agriculture, in chestnut restoration, the turn to emerging genetic and genomic technologies has been framed -- most notably by Powell -- as an approach that could supplant slower, more cumbersome breeding approaches:

In addition to being rather imprecise...backcross breeding requires many generations and thousand[s] of trees to produce individuals suitable for restoration. For those reasons, my many collaborators and I are focusing on a second approach, which relies on altering the chestnut tree's DNA in a much more exact way than traditional breeding and which has the potential to produce more fungus-resistant trees more quickly. (Powell, 2014: 71)

The projects funded by the FHI were also motivated by an interest in expediting the production of disease-resistant lines with "rapid and responsible innovation" (FHI, 2018). The results of that project include new leaf assays which enable the detection of blight-resistance in transgenic plants after one year, rather than five; new transformation techniques that carve a year off of the time it takes to develop potted plants from transformed embryos; and new somatic embryogenesis techniques that have "the potential to condense 50 years of breeding into 15 years" (FHI, 2018: 11).

However, the thrust for precision and efficiency in this case appears to principally emerge, not from an interest in cycling more capital, as has been argued in agriculture (Busch, 2010), but from the sense of crisis and urgency that have always characterized biodiversity conservation (Soulé, 1985). Crisis narratives have been used in calls for the adoption of biotechnology since its earliest formulation (Bud, 1998) and have been employed widely and critiqued heavily in relation to the value of genetically modified crops for addressing food security (Jansen and Gupta, 2009) and the stability of non-food crops such as cotton (Glover, 2010). The urgency of future problems and the unmatched ability of genetic tools to address them has also been a potent narrative in efforts to rescue American chestnut and other forest

species from extinction (Merkle et al., 2007; Wheeler and Sederoff, 2009). Reflecting on the work done by the FHI, Carlton Owen, President and CEO of the U.S. Endowment for Forests and Communities, said, “Forests are being lost at an alarming rate due to devastating insect and disease infestations, and we don’t have the luxury of time that affords using only 20th century tools to deal with 21st century challenges” (U.S. Endowment for Forests and Communities, March 8, 2018). Powell and TACF staff have both argued that the re-establishment of independent and evolving American chestnut populations requires returning the genetic diversity housed in remaining stump sprouts to the reproductive gene pool of the species by crossing them with blight-resistant backcross or transgenic trees. Most, if not all, sprouts in contemporary forests have regenerated from root systems that were established in the late 1800s or early 1900s (Paillet, 2002); over time, stumps lose this regenerative capacity, placing a biological timer on opportunities to rescue this genetic diversity. Additionally, the project arguably becomes socially less tractable as relationships to and memories of American chestnut are lost with each generation.

Although genetic technoscience has, in many ways, expedited the production of blight-resistant American chestnut germplasm, the goal of restoring the species across its native range, which covered some 180 million acres, will require large-scale production of seeds and trees. TACF’s seed orchards are not likely to be sufficient to keep up with the need for blight-resistant seeds, either for restoration or to satisfy public interest (Jacobs, 2007). Scientists involved in both the backcross and transgenic programs have expressed concern over the imminent bottleneck in the production of blight-resistant material for restoration and uncertainty about how exactly it might be resolved, although many of them suggest that commercial nurseries may play an important role. One scientist from SUNY-ESF said,

We're mostly molecular biologists, so we can produce a tree, and we can describe a tree, and we can produce a few trees, but we're not a tree production facility, and we never will be. We can talk about trees in the thousands, but meaningful restoration will be trees in the millions.

Realistically, producing that kind of number would mean contracting with really large-scale nurseries and a really different set of expertise than we have. (Andy Newhouse, May 9, 2017)

Like this scientist, many of the others we interviewed discussed nurseries primarily as a source of expertise in the cultivation and large-scale production of trees. However, nurseries are also businesses, and collaborations forged between TACF or SUNY-ESF and commercial nurseries may involve the establishment of new relationships to American chestnut as a commodity. In fact, one TACF scientist explained that there has been some reluctance to involve nurseries in the restoration project so far and that it may be attributable to mistrust of their commercial motives. Also in tension with a move towards the transformation of blight-resistant American chestnut into a commodity, TACF's Director of Science has suggested that broad release of blight-resistant trees to an open, free market may be at odds with the pursuit of restoration as an intentional and controlled project. The distribution of trees through nurseries, followed by a "Johnny Appleseed approach" to planting them, would limit TACF's ability to "be more involved, more heavy-handed, in distributing the trees in a large-scale way, in an intelligent way." He indicated that instead, TACF may want to work more systematically with large landowners in order to direct the spread of blight-resistance in the wild and monitor the success of restoration.

Commercialization

In the long history of efforts to resurrect American chestnut populations, industry interest and involvement have been minimal. In the early 20th century, American chestnut products, especially timber, tannins, and nuts, comprised a substantial portion of national markets (Freinkel, 2007). Facing the imminent demise of a species that featured prominently in multiple markets, in addition to its widespread subsistence use by homesteaders throughout the Appalachians, foresters recommended harvesting remaining chestnut in an attempt to both limit the spread of *C. parasitica* in the landscape and maximize short-term profit in the event that it could not be stopped (Freinkel, 2007). Although initial interest in preventing the decline of American chestnut may have been principally related to its market value, its loss was concurrent with a number of other changes in Appalachia that undermined industry investment in its resurrection; the forestry industry turned to new tree species, nut vendors started importing and growing European chestnuts, and the leather tanning industry adopted synthetic chemicals (Freinkel, 2007). Although the historical importance of markets for chestnut is often invoked as a prelude to contemporary

restoration efforts, today, restoration is primarily justified on the basis of its potential to restore lost aspects of Appalachian culture and ecology. As described previously, the initial impetus for a transgenic American chestnut tree came from the non-profit sector -- from the New York chapter of TACF -- not from industry, and the project continues to be oriented by motives that are more environmental than economic. As Powell has written (2014: 73):

We are not growing a genetically modified organism on cropland for profit; rather we are producing trees for restoration without monetary gain. Like researchers working on golden rice enriched with a precursor of vitamin A, we are motivated by the public good -- and the health of the forest. The EPA generally grants seed companies licenses to sell transgenic seeds, but in our case, we have no one to hold the license and nothing to sell. It is not clear what kind of alternative approval they would give us, but we are determined to set a precedent.

After multiple failed attempts by government bodies to control chestnut blight or generate blight-resistant hybrids, attention to American chestnut waned until the establishment of TACF as a non-profit dedicated to its restoration (Steiner et al., 2017). While agricultural companies are under pressure to develop products that will provide a high return on investments made by the company and shareholders, TACF has no imperative to recoup the “tens of millions of dollars from public and private sources [that have] been invested since the 1980s in the work of TACF and complementary research at universities and in federal and state agencies, mostly in the expectation of a genetic solution to chestnut blight” (Steiner et al., 2017: 332).

An additional dimension of commercialization described by STS scholars has been the adoption of practices in public science that reveal commercial logics and have typically been characteristic of businesses. As the team at SUNY-ESF prepares for the regulatory process, with hopes of large-scale distribution of their transgenic trees to follow, they initiated a crowdfunding campaign called the “10,000 Chestnut Challenge” in order to raise funds and support for their efforts. The appeal of crowdfunding in science may be partially driven by the neoliberal constriction of public funding for research (Hui and Gerber, 2015), and crowdfunding appears to both embody neoliberal faith in the wisdom of crowds and to

reinforce consumer-based activism. Consistent with the expectations of Lave et al. (2010), who suggest that neoliberal science is marked by deference to market mechanisms to decide intellectual disputes, unexpected levels of financial support in the 10,000 Chestnut Challenge and associated positive commentary in social media forums such as Facebook and Twitter, have been interpreted as evidence for broad public support of a transgenic approach to blight-resistance by Powell's team and the Development Office at SUNY-ESF (Harrison et al., 2017). However, this crowdfunding effort also aimed to establish an infrastructure for the future distribution and diversification of transgenic American chestnut trees. In the campaign, which was specifically designed to raise money for the production of 10,000 transgenic seeds, members of the public received a pure American chestnut seed for donating, as well as the promise of a transgenic seed, pending their federal deregulation. American chestnut is self-sterile and requires another, genetically distinct tree in its vicinity in order to produce seed. Donors were thus instructed to plant their native American chestnut seed now, in order to grow a large number of "mother trees" which might be receptive to the pollen of transgenic trees, once available. If successful, this process would generate large numbers of American chestnut seeds, half of which would be expected to carry the oxalate oxidase gene and be blight-resistant.

Explaining the uneven politics of genetic technoscience: Polanyi's double movement

Even though it does not embody a complete refutation of neoliberal patterns in science and technology, the application of genetic technoscience to the restoration of American chestnut provides ample ground for challenging the prevailing assumption that genetics and genomics are inherently or necessarily complicit in the accomplishment of neoliberal goals. As described previously, Winner (1980) demonstrated that while some technologies are inherently consistent with only particular arrangements of power, others are amenable to multiple political and economic structures; that means that some technologies are uneven in their political and economic consequences. The details of the American chestnut case lead us to conclude that genetic technoscience is one of these flexible technologies; it is not inherently neoliberal, but certainly convenient to the neoliberal project and amenable to being used to

further the extension of markets into human and non-human bodies in some contexts. While the theory of technological politics makes room for the politics of genetic technoscience in species restoration to deviate from the politics of genetic technoscience in agriculture, it does not explain *why* genetic technologies in this case resist important neoliberal patterns; it also does not explain why they reify others. Understanding how a technology that embodies “neoliberalism on the molecular scale” (McAfee, 2003: 203) in agriculture is able to eschew some of the defining characteristics of this political and economic project in the context of American chestnut restoration requires engaging with the uneven nature of neoliberalism itself.

Just as the politics of genetic technoscience can be constructed anew in different contexts, scholars, particularly in geography and political ecology have demonstrated that “neoliberalism is not monolithic” (Mansfield, 2004), but rather shaped by the political, cultural, and ecological realities of the settings in which it is enacted (Barnett, 2005; Lerner, 2003; O’Neill and Argent, 2005; Peck, 2004). Thus, neoliberalism unfolds differently in different places and times, and the neoliberal ideal often diverges from what have been referred to as “actually existing neoliberalisms” (Brenner & Theodore, 2002). As Mansfield (2004: 580) has written,

It is not a single, coherent entity spreading across the land (and sea), either to the good or demise (depending on one’s perspective) of people and environments everywhere. The particular forms that neoliberalism takes should not be taken as aberrant from an ideal, or as not really neoliberal. Instead, our understanding of neoliberalism needs to acknowledge that it is something created in practice, and that through practice, it becomes varied, fractured, and even contradictory... Real neoliberalism is not an unchanging and all-powerful force, but instead is a political project that incorporates, responds to, and shapes geographical, historical, sectoral, and even ecological variation.

Polanyi (1944) likewise insisted that the perfectly free markets of classical liberalism were a utopian ideal that could never be fully realized in practice. This is because efforts to completely disembod the economy from social controls as a self-regulating market and to transform human labor and the environment into

commodities to be bought and sold would inevitably be resisted by both society and nature. Block explains that “as the consequences of unrestrained markets become apparent, people resist; they refuse to act like lemmings marching over a cliff to their own destruction. Instead, they retreat from the tenets of market self-regulation to save society and nature from destruction” (Block, 2001: xxv). Polanyi (1944) described this phenomenon as a *double movement*; the first movement towards the marketization of everything is countered by a second movement that resists marketization. In response to this resistance, the liberal state establishes protective policies, including labor laws and tariffs, that insulate society and natural resources from the ills of unchecked capitalism.

Scholars have shown that this double movement also characterizes neoliberalism, which has been “beaten back in places by virulent resistance” against the removal of the state from environmental governance and its replacement with a free market (McCarthy and Prudham, 2004: 275). Castree (2010: 1744) has explained that a double movement occurs when “a market economy rubs up against various pre-existing moral economies and ‘unruly’ biophysical systems” (Castree, 2010: 1744). Concerns about nature and related political resistance have supported some of the most important oppositions to neoliberalism and unveiled its contradictions (McCarthy and Prudham, 2004), while biological resistance posed to marketization by ecologies and evolutionary processes has illustrated its limits. Social and biological resistance have likewise imposed limits on the ability of genetic technologies to expand the reach of neoliberalism or make nature less “fictitious” (Polanyi, 1944) and amenable to further privatization, commodification, and commercialization. These two origins of the double movement -- social and biological resistance -- provide a useful heuristic for considering the reasons that neoliberal patterns have been resisted as genetic technoscience has been employed in the restoration of American chestnut. Importantly, while the double movement in classical liberalism resulted in social protections provided by the state, under neoliberalism, in which the role of the state is diminished, resistance is increasingly responded to by non-governmental actors, civil society groups, and, perhaps, individual scientists, which act as “flanking mechanisms” (Castree, 2010), providing balm for the externalities of capitalism.

Social resistance to neoliberalism

Polanyi (1944) held that the subjection of human labor and nature to the market under liberal capitalism violates long-held beliefs about the exceptionality and sacredness of human and non-human life, and that this violation provides a major impetus for resistance to marketization. Much of the opposition to the use of genetic and genomic technoscience in agriculture has been in response to the privatization, through patents, of plant materials that have been stewarded and improved by indigenous and subsistence communities for centuries (Delborne & Kinchy, 2008; McAfee, 2003b). Indigenous groups throughout the world have been particularly active in promoting the notion of the “genetic commons” in an effort to resist the privatization, commodification, and commercialization of agricultural germplasm (Scharper and Cunningham, 2006). Efforts to protect the genetic commons have now been formalized in treaties including the Treaty to Share the Genetic Commons and the International Treaty on Plant Genetic Resources for Food and Agriculture, supported by the international authority of the Food and Agricultural Organization. The application of genetic technologies, particularly genetic engineering, to American chestnut restoration has been pursued with this legacy of the fraught history of its application to agriculture. Powell’s decision not to seek a patent on his Darling trees, the FHI’s commitment to transparent and publicly available science, and TACF’s historical resistance to collaboration with commercial nurseries might all be understood as reactions to the moral arguments that have been powerful in resisting genetic technoscience in agriculture.

It is important to note, however, that Powell has never indicated an explicit rejection of the privatization of American chestnut or other plant genetic resources. In fact, he and other scientists involved in American chestnut restoration have defended the right of corporations to patent the products of forest biotechnology; they simply see patented germplasm as inconsistent with a restoration program premised on the open and uncontrolled release of blight-resistant American chestnut into wild ecosystems. For that and the reasons described above, Powell’s decision to forego patent protection appears to be more practical than philosophical. However, in his presentation at an annual U.S. EPA - Region 2 Indian Nation Leaders Meeting, Powell indicated sensitivity to another “pre-existing moral

economy” (Castree, 2010: 1744), by invoking the notion of reciprocity. In that meeting, and in others since, Powell discussed a transgenic American chestnut as a way to give back to nature by quoting Robin Kimmerer, Professor of Environmental and Forest Biology and founding Director of the Center for Native Peoples and the Environment at SUNY-ESF. Speaking before the United Nations, Kimmerer (2015) stated that

We humans are more than consumers; we have gifts of our own to give to the Earth. We are scientists and artists and farmers and storytellers. We can join in the covenant of reciprocity, seeking what Onondaga Clan Mother Audrey Shenandoah called “Justice not only for ourselves, but justice for all of Creation.”

Powell’s use of this talk to frame his work as an act of reciprocity is echoed in narratives about the rationale for restoring American chestnut, a species whose presence in both social and ecological systems has been waning for a century. Although early efforts to protect American chestnut populations were undoubtedly motivated by an interest in maintaining the viability of economies based on chestnut, today, the motivations espoused by TACF and their collaborators for returning the species to its former niche are restorative in nature, rather than extractive. The organization focuses on the re-establishment of American chestnut as a mechanism for restoring forest ecosystems, lost biodiversity, cultural heritage, and even degraded minelands (TACF, 2018a). Whether or not arguments against privatizing the commons and for acts of reciprocity towards nature have been internalized by those involved in American chestnut restoration at SUNY-ESF, TACF, and FHI, their awareness of these moral imperatives and their power in thwarting the use of genetic technoscience in agriculture appear to be shaping the political economy of the technology in species restoration.

Biophysical resistance to neoliberalism

Scholars in political ecology have also demonstrated that biological and physical systems can impose limits on the ability of technological innovation to extend markets to nature. According to Robbins (2012), an apolitical view of technology concludes either that innovations drive social change or that social needs draw forth and shape innovations -- much like the technological and social determinism

challenged by STS scholars like Winner (1980). On the other hand, a political ecological approach draws attention to the ways in which innovations are a response to the limitations imposed by nature:

It is instead the very limits of the accumulation of capital and power set by non-human actors (e.g., seeds) that lead to economic and institutional change and the innovations that seek to overcome these limits. Dialectically, innovations, while not the drivers of change, become enrolled in power-laden networks of relations that create new opportunities to resist, rework, and reimagine nature/society relationships. (Robbins, 2012: 238)

American chestnut cannot be simply privatized, commodified, and commercialized with the application of genetic technoscience because it remains “[a] tree that was never tamed, a wild forest king whose dominion sprawled over more than two hundred million miles” (Freinkel, 2007: 15).

In the history of various approaches to protecting and restoring populations of American chestnut, the biology of the species has consistently complicated efforts to save it. Early measures to stop the spread of the fungus were widely unsuccessful, due to the biology of both the fungus and the tree. *C. parasitica* enters trees through wounds or fissures in the bark and colonizes the cambial tissue between the xylem and phloem of the tree’s vascular system (Powell, 2014). As a necrotrophic pathogen, chestnut blight produces a chemical – oxalic acid – that eats through the surrounding tissue, causing regional cell death in the tree and making room for fungal expansion. This interaction produces a perennial canker that prevents the flow of water and nutrients throughout the tree and ultimately kills it above the point of infection (Jacobs et al., 2013; Powell, 2014). The persistence of the fungal canker and the early development of both asexual and sexual fungal spores facilitated the rapid and ongoing proliferation and spread of *C. parasitica* (Jacobs et al., 2013), while the highly fissured bark of American chestnut trees and the apparent lack of inherent genetic resistance made them particularly susceptible to infection (Curry, 2014). Once attention turned to developing blight-resistant American chestnut trees, scientists encountered a long lifespan, delayed reproductive maturity, sectorial mutation, and self-sterility. Blight-resistant backcross trees expected to be developed in a few generations (Burnham, 1981) are still blighted 40 years later due to genetic recombination near the locus of blight resistance (Wheeler and Sederoff,

2009) and the difficulty of controlling the prolific, wind-dispersed pollen of both American and Chinese trees in breeding orchards. It turns out that “[r]eal life—as opposed to genetic formulae—exhibits both recalcitrance and resilience in response to interventions that attempt to finetune the molecular functions of organisms” (McAfee, 2003: 206).

The application of genetic technoscience to American chestnut restoration was initiated to overcome many of these constraints, but those innovations continue to work with and against the biology and ecology of the species. Although researchers at SUNY-ESF thought the production of blight-resistant trees would take five years, it ultimately took 27 (Zhang et al., 2013). Powell said,

It was much more difficult than we thought it would be. Chestnut is not a hybrid poplar; it’s not as easy to work with. I always tell people we had to build our boat before we went fishing. We had to develop all of the techniques to transform chestnut and regenerate it into a full tree before we actually started looking at genes. (William Powell, personal communication, May 9, 2017)

And they still have a long way to go before chestnut trees carrying the oxalate oxidase gene are ready for large-scale reintroduction. Transgenic American chestnut seedlings raised from tissue culture do not develop neatly into tall, straight trees because this process generates whole seedlings from individual plant cells that were otherwise destined to form a leaf or branch or root.

The difficulties posed to the privatization, commodification, and commercialization of American chestnut by the biology of the species might be overcome in time; indeed, similar kinds of biological resistance have been subdued in agricultural systems by scientific and political innovation (Kloppenburg, 2005). However, in this case, the primary challenge posed to neoliberalism by “unruly biophysical systems” (Castree, 2010: 1744) emerges from the very goal of the project, which is to return blight-resistant American chestnut populations to the species’ expansive historical range. Achieving this mission is, in many ways, fundamentally inconsistent with the “detailed control of people and things” characteristic of neoliberalism (Busch, 2010: 343) because it will require diversity and local adaptation in American chestnut germplasm, not to mention the maintenance or re-establishment of complex ecological relationships, particularly with pollinators, dispersers, and microbial communities. Thus, even where

reductionism and standardization are apparent in this project, they are necessarily temporary, eventually followed by mechanisms for diversifying and “rewilding” the germplasm developed in breeding orchards and laboratories. The ultimate release of blight-resistant American chestnut to natural ecological and evolutionary processes eliminates the need for and feasibility of human and market control over the conditions of reproduction for the species. This is a key difference between the open release of a genetically manipulated organism in biodiversity conservation as opposed to the use of biotechnologies in presumably contained agricultural systems; while IP and genetic technologies like terminator genes could be used to prevent the proliferation of the products of genetic technoscience in agriculture (Biermann and Anderson, 2017), these controls would critically undermine the goal of re-establishing independent and evolving American chestnut populations in Appalachian forests.

Making the market work

For Polanyi (1944), the double movement that characterizes liberal capitalism -- the social resistance and ultimately, social protections, precipitated by the ills of marketization -- is as much about making the market work as it is about challenging it. Mansfield (2004) has demonstrated this in fisheries, where regulatory intervention -- the anathema to free markets -- has been used to ensure the continuation of the market for Alaskan pollock by protecting the biological sustainability of fishing stocks and the economic viability of local communities. Because the double movement phenomenon has been useful in explaining the ability of genetic technoscience to resist neoliberalism in the context of American chestnut restoration, we must also consider the ways in which this resistance might be facilitating the persistence of markets for forest biotechnology, intentionally or not.

Although commercial actors were largely uninterested in American chestnut for some time, various portions of this restoration effort have now been funded by key industry players. Research at SUNY-ESF has been supported by many donors, including ArborGen, one of the largest global providers of both conventional and engineered tree seedlings for commercial forestry, and Weyerhaeuser, one of the largest forest products companies in the world (SUNY-ESF, 2018). Additionally, although the initial thrust for a transgenic American chestnut originated with TACF, as described previously, in 2009, the

project was taken up as a “test case” by the FHI. Even though “all funding for the FHI came from partners outside of any for-profit biotechnology companies to ensure the program’s objectives of transparency, independence, and maximizing societal benefit” (FHI, 2018), the initiative was run by the Institute for Forest Biosciences, which works with its partners, including ArborGen and Weyerhaeuser, to “accelerate the responsible use of forest biotechnologies” (IFB, 2018). Additionally, FHI was supported by Duke Energy, which has a growing interest in and commitment to the use of biofuels for energy production (Duke Energy, 2018); ArborGen has engineered a cold-tolerant eucalyptus tree that could be used for that purpose, given regulatory and public approval (Voosen, 2010). For these groups, American chestnut restoration provides a key example of the benevolent potential of forest biotechnology to rescue heritage tree species from threats associated with invasive pests and pathogens. Multiple scientists involved in American chestnut restoration expressed concerns about the co-optation of the transgenic approach to blight-resistance by those interested in the commercialization of other genetically engineered trees. One scientist said:

I knew we were being used... I knew the only reason [they] got interested in chestnut was to sell [genetic engineering] in trees. Companies are not interested in chestnut, but once they get that through regulation, it's going to be easier to get loblolly pine and eucalyptus and Douglas fir through. To me, it's kind of a Trojan horse that's supposed to grease the wheels. (TACF scientist, personal communication, March 30, 2017)

While not directly interested in American chestnut, commercial actors are interested in the technical and regulatory insights and achievements emerging from the American chestnut project, and the potential exists for this non-profit application of genetic technoscience to be used to smooth acceptance of applications that are more commercially-motivated (Harrison et al., 2017).

Conclusion

The ongoing application of genetic and genomic technologies to the restoration of American chestnut to its former niche and native range in the eastern United States is challenging patterns of neoliberal privatization, commodification, and commercialization described for the use of these

technologies in agriculture. The theory of technological politics reminds us that this is not necessarily unexpected; while some technologies are inevitably linked to certain political and economic arrangements, many others can be involved in the coproduction of a variety of political orders. This distinction matters, for, as Winner (1980: 134) has suggested, “[t]o know which variety of interpretation is applicable in a given case is often what is at stake in disputes, some of them passionate ones, about the meaning of technology for how we live.” While the political economy of American chestnut trees developed with genetic engineering and backcross breeding is distinctly un-neoliberal in significant ways, this project is deeply influenced by the neoliberal legacy of genetic technologies in agriculture and situated in scientific processes that embody clear market logics. However, Polanyi’s (1944) double movement insists that it is quite possible to be embedded in neoliberalism while challenging it, as conditions internal to the neoliberal project -- principally, the creation of “free, self-actualizing subjects” (Bondi and Laurie, 2005) -- leave room for meaningful resistance to the extension of markets to nature.

The American chestnut restoration effort is still developing, with important decisions still open about the privatization hybrid germplasm and commercialization of blight-resistant trees. The impact of this project on the political and economic future of forest biotechnology also remains to be seen. Still, even in its nascent stage, this project demonstrates the ways in which “pre-existing moral economies” and “unruly biophysical systems” (Castree, 2010: 1744) can provide substantial challenge to the neoliberalization of nature. Historical social resistance to the commodification of agricultural germplasm and biological resistance posed by the very nature of species restoration have precipitated political and economic decisions that are antithetical to the neoliberal patterns described in agriculture. As calls continue to increase for the use of emerging genetic and genomic technologies for addressing important problems in human health, biodiversity conservation, and even food security, critical scholars must remain committed to nuanced analyses and open to the possibility that technologies that support a given political economic structure in some contexts might be used to challenge that same order in others.

References

- Anagnostakis SL, Chen B, Geletka LM, and Nuss DL (1998) Hypovirus transmission to ascospore progeny by field-released transgenic hypovirulent strains of *Cryphonectria parasitica*. *Phytopathology* 88(7): 598–604. DOI: 10.1094/PHYTO.1998.88.7.598.
- Barnett C (2005) The consolations of ‘neoliberalism’. *Geoforum* 36(1): 7-12.
- Beauchamp C (2013) Patenting nature: a problem of history. *Stanford Technical Law Review* 16(2): 257-312.
- Biermann C and Anderson RM (2017) Conservation, biopolitics, and the governance of life and death. *Geography Compass* 11(10): e12329. DOI: 10.1111/gec3.12329.
- Block F (2001) Introduction. In: Polanyi K *The Great Transformation: The Political and Economic Origins of Our Time*. Boston: Beacon Press.
- Bondi L and Laurie N (2005) Introduction to Working the Spaces of Neoliberalism: Activism, Professionalisation and Incorporation. *Antipode* 37(3): 393-401.
- Brenner N and Theodore N (2002) Cities and the geographies of ‘actually existing neoliberalism’. *Antipode* 34(3): 349–379. DOI: 10.1111/1467-8330.00246.
- Brooks S (2015) Philanthrocapitalism, ‘pro-poor’ agricultural biotechnology and development. In Morvaridi B (ed.) *New Philanthropy and Social Justice: Debating the Conceptual and Policy Discourse*. Bristol: Policy Press, 101-116.
- Bud R (1998) Molecular biology and the long-term history of biotechnology. In: Thackray A (ed.) *Private Science: Biotechnology and the Rise of the Molecular Sciences*. Philadelphia: University of Pennsylvania Press, 3-19.
- Burnham CR (1981) Blight-resistant American chestnut: There’s hope. *Plant Disease* 65(6): 459-460.
- Burnham CR (1988) The restoration of the American Chestnut: Mendelian genetics may solve a problem that has resisted other approaches. *American Scientist* 76(5): 478–487.
- Busch L, Lacy WB, Burkhardt J, and Lacy LR (1991) *Plants, power, and profit: social, economic, and ethical consequences of the new biotechnologies*. Cambridge, MA: Blackwell.
- Busch L (2010) Can fairy tales come true? The surprising story of neoliberalism and world agriculture. *Sociologia Ruralis* 50(4): 331–351. DOI: 10.1111/j.1467-9523.2010.00511.x.
- Castree N (2010) Neoliberalism and the Biophysical Environment 1: What ‘Neoliberalism’ is, and What Difference Nature Makes to it: Neoliberalism and the biophysical environment 1. *Geography Compass* 4(12): 1725–1733. DOI: 10.1111/j.1749-8198.2010.00405.x.
- Cooper ME (2008) *Life as surplus: Biotechnology and capitalism in the neoliberal era*. Seattle: University of Washington Press.

- Curry HA (2014) Radiation and restoration; or, how best to make a blight-resistant chestnut tree. *Environmental History* 19(2): 217–238. DOI: 10.1093/envhis/emu001.
- Delborne JA and Kinchy AJ (2008) Genetically modified organisms. In Restivo, S. and Denton, P. H. (Eds.), *Battleground Science and Technology, Volume 1*. Westport, CT: Greenwood Press, 182–195.
- Duke Energy (2018). Bioenergy. Available at: <https://www.duke-energy.com/our-company/environment/renewable-energy/biopower> (April 4, 2018)
- Evans JA (2010) Industry collaboration, scientific sharing, and the dissemination of knowledge. *Social Studies of Science* 40(5): 757–791. Available at: <http://www.jstor.org/stable/25746362>.
- Fang G-C, Blackmon BP, Staton ME, et al. (2013) A physical map of the Chinese chestnut (*Castanea mollissima*) genome and its integration with the genetic map. *Tree Genetics & Genomes* 9(2): 525–537. DOI: 10.1007/s11295-012-0576-6.
- Forest Health Initiative (FHI) (2018) Forest Health Initiative: A retrospective look. Rapid and responsible innovation. Available at: http://foresthealthinitiative.org/resources/FHI_Retrospective_Look.pdf
- Foucault M (2008) *The birth of biopolitics*. New York: Palgrave Macmillan.
- Freinkel S (2007) *American chestnut: the life, death, and rebirth of a perfect tree*. Berkeley: University of California Press.
- Friedman M (2009) *Capitalism and freedom*. Chicago: University of Chicago Press.
- Glover D (2010) Exploring the resilience of Bt cotton’s ‘pro-poor success story’. *Development and Change* 41(6): 955–981. DOI: 10.1111/j.1467-7660.2010.01667.x.
- Haraway D (1997) *Modest Witness@Second Millennium. FemaleMan Meets OncoMouse: Feminism and Technoscience*. New York: Routledge.
- Harrison R, Kinchy A, and Rabinow L (2017) Genetically engineered food for a hungry world: A changing political economy. In Tyfield D, Lave R, Randalls S, and Thorpe C (eds.) *The Routledge Handbook of the Political Economy of Science*. London: Taylor & Francis, 213–223.
- Harvey D (2007) *A brief history of neoliberalism*. New York: Oxford University Press.
- Hebard FV (2005) The backcross breeding program of the American Chestnut Foundation. *Journal of the American Chestnut Foundation* 19(2):55–77
- Himley M (2008) Geographies of environmental governance: The nexus of nature and neoliberalism. *Geography Compass* 2(2): 433–451. DOI: 10.1111/j.1749-8198.2008.00094.x.
- Hoeyer K (2007a) The role of ethics in commercial genetic research: Notes on the notion of commodification. *Medical Anthropology* 24(1): 45–70. DOI: 10.1080/01459740590905642.
- Hoeyer K (2007b) Person, patent and property: A critique of the commodification hypothesis. *BioSocieties* 2(3): 327–348. DOI: 10.1017/S1745855207005777.

- Holtz CT, Tull AR, Merkle SA (2016) Influence of species and hybrid status on induction of somatic embryogenesis in *Castanea*. *Canadian Journal of Forest Research* 47(3): 382-388. DOI: 10.1139/cjfr-2016-0362
- Hui JS and Gerber EM. (2015) Crowdfunding science: Sharing research with an extended audience. In *Proceedings of the 18th ACM Conference on Computer Supported Cooperative Work & Social Computing*. ACM, 31-43.
- Institute for Forest Bioscience (IFB) (2018) Partners. Available at: <https://forestbio.org/IFB/partners/> (April 4, 2018)
- Jacobs DF (2007) Toward development of silvical strategies for forest restoration of American chestnut (*Castanea dentata*) using blight-resistant hybrids. *Biological Conservation* 137(4): 497–506. DOI: 10.1016/j.biocon.2007.03.013.
- Jacobs DF, Dalglish HJ and Nelson CD (2013) A conceptual framework for restoration of threatened plants: the effective model of American chestnut (*Castanea dentata*) reintroduction. *New Phytologist* 197(2): 378–393. DOI: 10.1111/nph.12020.
- Jansen K and Gupta A (2009) Anticipating the future: ‘Biotechnology for the poor’ as unrealized promise? *Futures* 41(7): 436–445. DOI: 10.1016/j.futures.2009.01.008.
- Kimmerer R (2016) Harmony with Nature; Fifth Annual Conference at the United Nations. *Kosmos* XV(2): 54-65. Available at: <http://www.kosmosjournal.org/article/harmony-with-nature/>
- Kleinman DL (1998) Untangling Context: Understanding a University Laboratory in the Commercial World. *Science, Technology, & Human Values*, 23(3), 285–314.
- Kleinman DL and Vallas SP (2001) Science, Capitalism, and the Rise of the “Knowledge Worker”: The Changing Structure of Knowledge Production in the United States. *Theory and Society*, 30(4), 451–492.
- Kloppenborg JR (2005) *First the seed: The political economy of plant biotechnology*. Madison, WI: University of Wisconsin Press.
- Krimsky S (1991) *Biotechnics & society: the rise of industrial genetics*. New York: Praeger.
- Kubisiak TL, Hebard FV, Nelson CD, et al. (1997) Molecular mapping of resistance to blight in an interspecific cross in the genus *Castanea*. *Phytopathology* 87(7): 751–759. DOI: 10.1094/PHYTO.1997.87.7.751.
- Kubisiak TL, Nelson CD, Staton ME, et al. (2013) A transcriptome-based genetic map of Chinese chestnut (*Castanea mollissima*) and identification of regions of segmental homology with peach (*Prunus persica*). *Tree Genetics & Genomes* 9(2): 557–571. DOI: 10.1007/s11295-012-0579-3.
- Larner W (2003) Neoliberalism? *Environment and Planning D: Society and Space* 21(5): 509–512. DOI: 10.1068/d2105ed.
- Latour B (1987) *Science in Action: How to Follow Scientists and Engineers Through Society*. Cambridge, MA: Harvard University Press.

- Lave R, Mirowski P and Randalls S (2010) Introduction: STS and Neoliberal Science. *Social Studies of Science* 40(5): 659–675. DOI: 10.1177/0306312710378549.
- Mansfield B (2004) Rules of privatization: contradictions in neoliberal regulation of North Pacific fisheries. *Annals of the Association of American Geographers* 94(3): 565–584.
- McAfee K (2003) Neoliberalism on the molecular scale: Economic and genetic reductionism in biotechnology battles. *Geoforum* 34(2): 203–219. DOI: 10.1016/S0016-7185(02)00089-1.
- McCarthy J and Prudham S (2004) Neoliberal nature and the nature of neoliberalism. *Geoforum* 35(3): 275–283. DOI: 10.1016/j.geoforum.2003.07.003.
- Merkle SA, Andrade GM, Nairn CJ, et al. (2007) Restoration of threatened species: a noble cause for transgenic trees. *Tree Genetics & Genomes* 3(2): 111–118. DOI: 10.1007/s11295-006-0050-4.
- Newhouse AE, Spitzer JE, Maynard CA, Powell WA (2014) Chestnut leaf inoculation assay as a rapid predictor of blight susceptibility. *Plant Disease* 98(1): 4–9. DOI: 10.1094/PDIS-01-13-0047-RE.
- O'Neill PH and Argent N (2005) Neoliberalism in antipodean spaces and times: an introduction to the special theme issue. *Geographical Research* 43(1): 2-8.
- Otero G and Pechlaner G (2008) Latin American agriculture, food, and biotechnology: Temperate dietary pattern adoption and unsustainability. In Otero G (ed.) *Food for the few: Neoliberal globalism and biotechnology in Latin America*. Austin, TX: University of Texas Press, 31-56.
- Paillet FL (2002) Chestnut: history and ecology of a transformed species. *Journal of Biogeography* 29(10–11): 1517–1530. DOI: 10.1046/j.1365-2699.2002.00767.x
- Pechlaner G and Otero G (2008) The third food regime: Neoliberal globalism and agricultural biotechnology in North America. *Sociologia Ruralis* 48(4): 351–371. DOI: 10.1111/j.1467-9523.2008.00469.x.
- Peck J (2004) Geography and public policy: constructions of neoliberalism. *Progress in human geography* 28(3): 392-405.
- Polanyi K (1944) *The Great Transformation: The Political and Economic Origins of Our Time*. Boston: Beacon Press.
- Powell W (2014) The American chestnut's genetic rebirth. *Scientific American* 310(3): 68–73. DOI: 10.1038/scientificamerican0314-68.
- Robbins P (2012) *Political ecology: A critical introduction*. West Sussex: Wiley-Blackwell.
- Scharper SB and Cunningham H (2006) The Genetic Commons: Resisting the neoliberal enclosure of life. *Social Analysis* 50(3): 195-202. DOI: 10.3167/015597706780459403
- Schurman R and Munro WA (2010) *Fighting for the Future of Food: Activists versus Agribusiness in the Struggle over Biotechnology*. Minneapolis: University of Minnesota Press.

- Sisco PH, Kubisiak TL, Cassasoli M, et al. (2004) An improved genetic map for *Castanea dentata*/*Castanea mollissima* and its relationship to the genetic map of *Castanea sativa*. *Acta Horticulturae* 693: 491-496. DOI: 10.17660/ActaHortic.2005.693.63
- Soulé ME (1985) What is conservation biology? *BioScience* 35(11): 727-34.
- Steiner KC, Westbrook JW, Hebard FV, Georgi LL, Powell WA, and Fitzsimmons SF (2016) Rescue of American chestnut with extraspecific genes following its destruction by a naturalized pathogen. *New Forests* 48:317-336. DOI: 10.1007/s11056-016-9561-5.
- SUNY-ESF (2018) Support the project: The American Chestnut Research and Restoration Project. Available at: <http://www.esf.edu/chestnut/funding.htm> (April 4, 2018)
- The American Chestnut Foundation (TACF) (2017) 2017-2027 Strategic Plan. Available at: <https://www.acf.org/wp-content/uploads/2017/09/WEB-Strategic-Plan-090617.pdf?x86657> (April 2, 2018)
- The American Chestnut Foundation (TACF) (2018a) About TACF. Available at: <https://www.acf.org/about-us/> (April 2, 2018)
- The American Chestnut Foundation (TACF) (2018b) The American Chestnut Foundation Germplasm Agreement. Available at: <https://www.acf.org/about-us/germplasm-agreement/> (April 2, 2018)
- U.S. Endowment for Forestry and Communities (2018, March 8). Report recaps successful “braided” approach to scientific advances for forest health. Press Release. Available at: http://www.usendowment.org/images/FHI_Press_release_1_030218.pdf
- Voosen P (2010) Genetically modified forest planned for U.S. southeast. *Scientific American*. Available at: <https://www.scientificamerican.com/article/eucalyptus-genetically-modified-pine-tree-southwest-forest/> (April 2, 2018)
- Wheeler N and Sederoff R (2009) Role of genomics in the potential restoration of the American chestnut. *Tree Genetics & Genomes* 5(1): 181–187. DOI: 10.1007/s11295-008-0180-y.
- Winner L (1980) Do Artifacts Have Politics? *Daedalus* 109(1): 121-136.
- Zhang B, Oakes AD, Newhouse AE, Baier KM, Maynard CA, and Powell WA (2013) A threshold level of oxalate oxidase transgene expression reduces *Cryphonectria parasitica*-induced necrosis in a transgenic American chestnut (*Castanea dentata*) leaf bioassay. *Transgenic Research* 22(5): 973–982. DOI: 10.1007/s11248-013-9708-5.

CHAPTER 4

ANTICIPATORY GOVERNANCE AND THE REORIENTATION OF CONSERVATION IN THE ANTHROPOCENE: LESSONS FROM AMERICAN CHESTNUT RESTORATION

Abstract

The direction, scale, pace, and irreversibility of contemporary environmental changes challenge conservation approaches and paradigms that are based on the preservation of historical, baseline conditions and have resulted in calls for a reorientation of biodiversity conservation towards the future. This reorientation has proven difficult as it requires fundamental changes in the field's policies, practices, and philosophies. This chapter suggests that the framework of anticipatory governance, as developed by scholars in science and technology studies (STS), offers conservation science an approach to future-oriented decision-making that is well-equipped to consider both novel environmental conditions and novel conservation approaches that incorporate emerging genetic technologies. Defined by a combination of foresight, engagement, and integration, anticipatory governance is consistent with ongoing conversations in conservation science about the need for a long-term perspective, the engagement of local communities, and the inclusion of social science insights in conservation planning. It diverges from other frameworks, however, in its temporal approach, as it emphasizes the social shaping of technologies and interventions before they are implemented. Drawing on three years of ethnographic research, including participant observation and in-depth interviews, this chapter distills three key constraints on the adoption of a future orientation by organizations involved in American chestnut restoration and then describes how these constraints have been partially circumvented by activities that embody the dimensions of anticipatory governance. Future-oriented and long-term anticipations have been limited in American chestnut restoration by commitments to a particular vision of the historical importance of the species; practical limits in expertise and resources; and the confines of biotechnology policy. However, as scientists involved in this effort have engaged in dialogues with public groups and collaborations with citizen scientists and other experts, their capacity to anticipate and prepare for the social and ecological ramifications of their work have been expanded.

Introduction

In the last decade, conservation science has become increasingly aware of the reality and implications of ongoing environmental change (Williams et al., 2015) and human influence on even presumably untouched landscapes (Boivin et al., 2016). Collectively denoted by the contested, but captivating term Anthropocene (Buck, 2015), these changes have prompted numerous calls for a reorientation of biodiversity conservation away from the maintenance or re-creation of pre-disturbance or “natural” conditions and towards the protection of systems that will be resilient in an uncertain and unpredictable future (Choi, 2007; Corlett, 2016a). This reorientation has proven difficult as it requires fundamental changes in the field’s policies, practices, and philosophies. Kareiva and Fuller (2016) recently suggested that, as it attempts to prepare for and orient towards the future, conservation might look to the business sector for effective approaches to resource management in dynamic systems, where uncertainty and risks are high and surprises and shocks are likely. In particular, they point to the “act, sense, respond” approach of start-up businesses as a particularly useful model for conservation governance in the Anthropocene because it is a learning system that emphasizes change over constancy and encourages innovation and experimentation rather than precautionary inaction. They argue that this approach is especially vital for overcoming bias against novel conservation approaches, such as genetic rescue (Whiteley et al., 2015), assisted evolution (van Oppen et al., 2015), or facilitated adaptation (Thomas et al., 2013), that incorporate potentially disruptive genetic technologies.

For some conservationists, a reorientation towards the future entails a dramatic shift in the goals and techniques of biodiversity protection in ways that accept and channel human influence on natural systems rather than attempt to erase it (Corlett, 2016b; Kareiva et al., 2012; Marris, 2011). Advances in genetic science, including gene editing, gene drives, and synthetic biology, and related techniques such as cloning and somatic embryogenesis, have opened new avenues for this kind of “intervention ecology” (Hobbs et al., 2011) and promise to revolutionize the potential for directly manipulating the genetic composition of threatened plant and animal populations in order to save them (Corlett, 2016b; Kumar, 2012; Johnson et al., 2016; Taylor & Gemmill, 2016). While some scientists and conservationists have

argued for early exploration of the utility of these emerging genetic technologies for addressing biodiversity loss (Corlett, 2016b; Redford, Adams, & Mace, 2013), others have specifically spoken against proposals to use them in conservation (Civil Society Working Group on Gene Drives, 2018). Major concerns center on their ability to affect shared environments, to have social and ecological impacts that cross sovereign borders, and to be irreversible. Given the novelty, uncertainty, and complexity of these technologies, a number of leaders in conservation science and policy have more broadly warned that existing regulatory structures are not equipped to evaluate their risks or to govern their uncontained use in natural systems (Civil Society Working Group on Gene Drives, 2018). Standard regulatory tools like ecological risk assessment may be appropriate for quantifying the probability of long-term, irreversible impacts of technologies such as gene drives (NASEM, 2016), but they cannot be used to evaluate no-analog systems or social values (Sarewitz, 2015).

As the scale on which conservation interventions can impact shared environments increases, and in a context in which existing regulatory frameworks are insufficient, there is a need for an approach to conservation governance that can anticipate and prepare for the ways in which these novel interventions might intersect with complex social-ecological systems. In this paper, we argue that the framework of anticipatory governance, as developed by scholars in science and technology studies (STS), offers conservation science an approach to future-oriented decision-making that, unlike the experimental approach of business, is equipped to anticipate and address many of the social and ecological issues raised by the use of these technologies in wild systems *before* they are used. This *a priori* attention to possible futures is essential for the governance of conservation interventions that may precipitate both novel and irreversible changes to shared environments. Developed primarily within the context of nanotechnology at a time when that science was largely theoretical (Barben et al., 2008), anticipatory governance is particularly well-suited for conditions in which knowledge gaps and the potential for controversy are substantial. Rather than stifling technological innovation or fostering it for its own sake, anticipatory governance draws on foresight, public engagement, and the integration of experts across the social and natural sciences to direct the development and use of emerging technologies toward ends that are socially

responsible and just (Barben et al., 2008). This kind of guidance may be especially important before a potential merger between conservation and genetic technoscience, as both fields have been independently subject to heavy critique for their tendency to be culturally inappropriate; short-sighted and narrowly focused; and embedded in political-economic systems that benefit the powerful and dispossess the vulnerable.

The following section describes the framework of anticipatory governance and the ways in which related scholarship maps onto ongoing conversations in conservation science about the need for a long-term perspective, the engagement of local communities, and the expansion of social science in conservation science and practice. We then explore both limitations on and the potential for anticipatory or future-oriented conservation through an empirical case study of efforts to introduce populations of blight-resistant American chestnut (*Castanea dentata* (Marsh.) Borkh.) trees developed through genetic engineering and backcross breeding to forests of the eastern United States. The breadth and depth of questions asked about the potential future impacts of these trees are constrained in three key ways: 1) scientists and organizations involved in this project are committed to particular -- and problematic -- visions of the past of American chestnut as a baseline for restoration; 2) these organizations are subject to practical limits in time, resources, and expertise; and 3) the policies which apply to these trees only consider certain kinds of scientific risks and have not yet been applied to an organism designed for uncontained, wild release. However, the anticipations of researchers and conservationists involved in American chestnut restoration have been expanded as they have participated in dialogues and collaborations with members of the public and experts in other fields. These activities have both improved the science of American chestnut restoration and prompted those involved in this effort to consider the potential long-term social and ecological consequences of their work.

Anticipatory governance

The notion of anticipatory governance has been employed in distinct ways in a number of disparate fields, ranging from environmental studies to public administration. Though its specific use

varies, the concept consistently refers to an approach to decision-making that is both future-oriented and decentralized, with authority distributed across multiple actors, rather than situated solely within governments (Karinen & Guston, 2009). This approach focuses on the many mechanisms that control -- or *govern* -- issues of collective concern, especially in contexts in which the impacts of interventions are politically and scientifically uncertain and potentially very long-term (Karinen & Guston, 2009). As defined by scholars in science and technology studies (STS), “anticipatory governance comprises the ability of a variety of lay and expert stakeholders, both individually and through an array of feedback mechanisms, to collectively imagine, critique, and thereby shape the issues presented by emerging technologies before they become reified in particular ways” (Barben et al., 2008: 992-993). The undergirding philosophy of anticipatory governance is thus that decisions made about the design, development, and deployment of technologies in the present should be based upon democratic consideration of their potential future impacts.

The idea that interventions are not determined, but can and should be collaboratively shaped based on new information, resonates with the concept of adaptive governance, now common in conservation scholarship and practice. Developed to account for the dynamic, complex, and uncertain nature of ecological and environmental systems, adaptive governance is increasingly used in “situation[s] where the science is contextual, knowledge is incomplete, [and] multiple ways of knowing and understanding are present” (Gunderson & Light, 2006: 325). Like anticipatory governance, adaptive governance emphasizes the incorporation of emerging knowledge, anticipation of future risks, inclusion of diverse stakeholders, and systematic reflection on the performance of interventions (Armitage et al., 2007; Lockwood et al., 2010). However, a key difference in these frameworks is that anticipatory governance acknowledges and attempts to shape the decision-making processes that happen upstream, before technologies are employed or initiatives are put in place. While adaptive governance focuses on making changes in real time, anticipatory governance builds on constructive technology assessment, an approach that “aimed at reducing the costs of trial and error inherent in incrementalist policy and enabling more robust decision-making in the absence of the predictability of outcomes” (Karinen & Guston, 2009:

221). This temporal shift in anticipatory governance is also motivated by awareness of the potential for technological lock-in, in which the ability to change the course of innovations is diminished over time as they become incorporated into social, political, and physical systems; anticipatory governance thus aims to shape technologies while such shaping is still possible (Karinen & Guston, 2009).

Barben et al. (2008) identified three key challenges to this upstream “social shaping” of technologies: the *foresight* to consider the ramifications of technologies that remain largely hypothetical; the *engagement* of public audiences who generally have little knowledge of emerging technologies or their specific applications; and the *integration* of social science into natural science research that has long been rooted in notions of self-governance and scientific autonomy. These challenges have provided the foundation of a research program around anticipatory governance (Guston, 2014) as well as a framework for its implementation that has been adopted by scholars in diverse arenas (e.g. Kokotovich & Kuzma, 2014). Importantly, anticipatory governance emphasizes the combination, or *ensemblization*, of foresight, engagement, and integration, insisting that these processes ought to occur in concert, rather than piecemeal, because they are mutually reinforcing (Guston, 2014). For example, engagement and integration enable better foresight, but foresight also enables better engagement and integration.

Foresight

Achieved through a wide variety of methods, foresight refers to activities that aim to increase reflexivity in technoscientific projects by prompting developers, regulators, and end users to consider the long-term implications of science and technology. Component activities may include scenario development, technology assessment, goal-setting, visioning, and embedded dialogue, among others (Guston, 2014). Importantly, these anticipatory activities are not about predicting or divining the future, but about collecting information, including information about knowledge gaps, in ways that enable preparing broadly for an unknown and unknowable future (Guston, 2014). In the past decade, increasing attention has been given to the role of strategic foresight (Cook et al., 2014; Peterson et al., 2003) and scenario planning (Kass et al., 2011) in conservation. Cook et al. (2014) have argued that foresight activities can improve the ability of conservation decision-makers to minimize the negative impacts of

environmental change and to maximize the positive ones for species of concern. This is especially true for no-analog systems in which the future substantially deviates from the past. Consistent with perspectives on foresight in STS, in conservation, a “robust strategic foresight process systematically considers a range of possible, probable, or desirable futures, the hidden assumptions that underlie these futures, their potential consequences for policies and decisions, and the actions that might promote more desirable futures” (Cook et al., 2014: 532). However, foresight tools such as horizon scanning and scenario planning remain underutilized in conservation planning (Kass et al., 2011), and where present, are often used in isolation rather than as one component of broader, future-oriented practice (Cook et al., 2014), or an *ensemble*.

Engagement

Although foresight activities are oriented towards enhancing the reflexivity of scientists in particular, they are explicitly democratic and deliberative, “not so much directed at channeling scientific prophesy as they are at amplifying the still, small voices less often heard in the innovation process” (Guston, 2014: 229). The engagement of diverse stakeholders in anticipatory governance is both practical and normative. Practically, the generation of new insights in foresight activities is contingent upon the inclusion of diverse sets of expertise and perspectives, beyond the groups that are routinely involved in articulating the benefits and risks of given technologies or interventions (Cook et al., 2014). Sarewitz (2015) insists that “opening up questions of risk to democratic debate is on the whole good for science and innovation” and provides as evidence the heightened attention given to the safety of nuclear reactors in the United States, where the public was involved in discussions about the technology. A normative imperative for engagement emerges from the idea that visions of the future establish “material trajectories of life that unfold *as anticipated by those speculative processes*” (Adams et al., 2009: 248) and the notion that technological choices constitute world-making (Winner, 1986). Anticipatory governance is thus intentionally participatory, providing a diversity of actors with some say in what shape the world will take and what role individual emerging technologies will play in it (Guston, 2012; 2014). In conservation, stakeholder engagement is increasingly pursued because local communities stand to be directly impacted

by conservation programs, because they have kinds of expertise not captured in scientific assessments, and because program success or efficiency often hinges on their participation, support, or acceptance (Sterling et al., 2017). Consistent with the claims of anticipatory governance, this kind of engagement has been most impactful in conservation when it has been initiated early, frequently, and iteratively, incorporating different engagement mechanisms and different stakeholders over time (Jolibert & Wesselink, 2012; Sterling et al., 2017).

Integration

Anticipatory governance engages diverse publics in foresight activities in order to expand the kinds of issues that are considered in the process of technical research, specifically intending to foster attention to the societal and ethical dimensions of technologies. Another mechanism for the integration of social concerns into technoscientific research has been the placement of social scientists or humanists in laboratories. Through a variety of “collaboratively developed feedback mechanisms,” these researchers “stimulate a more self-critical approach to knowledge generation” (Barben et al., 2008: 988) by prompting scientists to explicitly consider the tacit assumptions and values that become embedded in their science (Fisher et al., 2006). Integration has also been achieved through collaborations between different sectors, such as private and public organizations and the involvement of citizens in scientific projects (Kearnes et al., 2006). These activities can result in the “midstream modulation” of scientific research and technological development, or changes that occur between upstream processes like problem formulation and downstream outcomes (Fisher and Schuurbiens, 2013). The importance of social science to conservation biology has been apparent since the field was first established (Soulé, 1985) and calls continue to be issued for more attention to human dimensions in conservation practice (Bennett et al., 2017). However, as Bennett et al. (2017) have argued, partially due to the diversity of social science disciplines, the integration of social scientists into conservation projects remains limited by a lack of understanding among natural scientists about what social scientists do and how they can contribute. Additionally, while it is widely recognized that conservation is an endeavor ultimately grounded in

human values, the extent to which conservation should be influenced by societal priorities has been contested (e.g. Soulé, 2013; Kareiva et al., 2012).

Towards the anticipatory governance of biodiversity conservation

The vocabulary and vision of anticipatory governance have been applied in a variety of contexts (Guston, 2014), including national security (Fuerth, 2009) and synthetic biology (Kuzma & Tanji, 2010). More recently, scholars in sustainability and resilience studies have begun to explore the applicability of anticipatory governance to the management of ecosystem services, particularly water resources, under climate change (Boyd et al., 2015; Vlieg & Zandvoort, 2013). These studies have demonstrated both the potential of anticipatory governance and the challenges associated with its implementation (Boyd et al., 2015). Although calls have been made in multiple fields, including psychology, anthropology, and economics, for a shift from past- to future-oriented analysis, research has yet to systematically consider the conditions and structures that are necessary for anticipatory action in practice (Poli, 2014). The following sections describe an empirical case study of efforts to restore populations of blight-resistant American chestnut trees to forests of the eastern United States. Through this case, we identify three key constraints on future-oriented or anticipatory conservation practice, including the historically-based vision and goals of American chestnut restoration; practical limitations in time, resources, and expertise; and the policies that bear, or do not bear, on genetically engineered and hybrid trees. Finally, we explore the ways in which anticipatory activities that embody ensembles of foresight, engagement, and integration have made some progress in overcoming these constraints.

Case background: American chestnut restoration

Once abundant in forests from Maine to Georgia and central in economies and cultures throughout the Appalachian mountains, American chestnut was brought to functional extinction by an introduced fungal pathogen in the early 1900s (Freinkel, 2007). Likely imported along with Japanese chestnut trees through ports in New York and California, chestnut blight (*Cryphonectria parasitica*) colonizes and induces regional cell death in the vascular system of trees; the resulting perennial canker

prevents the flow of water and nutrients throughout the tree and ultimately kills it above the point of infection (Jacobs et al., 2013). Due to the density of American chestnut in the landscape and the lack of native resistance to the pathogen, *C. parasitica* spread rapidly throughout the entire range of American chestnut in mere decades, transforming a population of over four billion large canopy trees (Gravatt, 1949) into a population of around 400 million understory sprouts (Dalglish et al., 2015). American chestnut sprouts continue to regenerate from the root collars of old stumps, but they rarely flower and fruit before being killed by chestnut blight, which remains ubiquitous in the landscape. While American chestnut is still relatively abundant and some portion of its gene pool still exists (Huang et al., 1998), its inferred ecological functions are believed to have stalled, and without sexual reproduction, it remains evolutionarily frozen in the early 1900s. As such, efforts to restore the species to its former dominance sit at a nexus between multiple forms of resurrection science, including ecological restoration, species reintroduction, facilitated adaptation, re-wilding, and de-extinction.

Current strategies to resurrect viable, evolving American chestnut populations include attempts at biological control using hypovirulent strains of the pathogen (Milgroom & Cortesi, 2004), as well as both intra- and interspecies breeding and trans- and cisgenic engineering of American chestnut trees (reviewed in Jacobs et al., 2013; Steiner et al., 2017). None of these approaches have yet resulted in trees ready for large-scale reintroduction, but “potentially blight-resistant” trees carrying resistance genes from Chinese chestnut have been developed through backcross breeding by the non-profit American Chestnut Foundation (TACF) and are currently planted on almost 1,200 acres across 680 locations throughout the species’ native range (TACF, 2018). Additionally, in cooperation with the New York Chapter of TACF, researchers at the State University of New York, College of Environmental Science and Forestry (SUNY-ESF) have used genetic engineering to transfer a gene from wheat into the American chestnut genome. This gene codes for an enzyme that neutralizes the destructive acid produced by *C. parasitica* and thus allows American chestnut trees carrying the gene to tolerate blight infection (Powell, 2014). Two transgenic events incorporating this gene are expected to undergo consideration for federal deregulation in the United States under the Coordinated Framework for Regulation of Biotechnology this year, with

applications for release in Canada to follow shortly thereafter (William Powell, personal communication, October 7, 2017). If approved for open release, the transgenic American chestnut developed at SUNY-ESF is poised to become the first genetically engineered organism released into wild environments for conservation purposes. As such, this project is positioned to set regulatory and public perception precedents for other conservation efforts that make use of genetic technologies.

Research methods

This paper is informed by three years of mixed-method qualitative social science research on American chestnut restoration. Ten semi-structured, in-depth interviews were conducted in person and by phone in 2017 with scientists involved in American chestnut restoration. Because we were specifically interested in understanding the perspective and activities of TACF and the American Chestnut Research and Restoration Project at SUNY-ESF as conservation organizations, we targeted scientists that are officially affiliated with and central to their operation. These conversations broadly focused on how scientists involved in American chestnut restoration understand the past, present, and future of efforts to resurrect this species. Interview questions explored the ways in which a variety of experts and public groups are included in restoration science and practice; key uncertainties about American chestnut and its restoration; and visions and concerns about the future of American chestnut and eastern forests. Interviews were audio recorded for accuracy and partially transcribed in MaxQDA, a qualitative data analysis software. The staffs at TACF and the American Chestnut Research and Restoration Project at SUNY-ESF are small, each comprised of less than 20 people. However, TACF collaborates with a wide range of university scientists who apply their expertise in areas such as tree genetics, forest ecology, and silviculture to understanding the past and future of American chestnut. We had many informal conversations with these individuals and reviewed their published work on American chestnut. This paper is also informed by participant-observation at three annual meetings of TACF, as well as an annual U.S. EPA - Region 2 Indian Nation Leaders Meeting, at which the transgenic American chestnut was

discussed. We also visited American chestnut breeding orchards and restoration locations in Meadowview, VA and Portland, ME and laboratories and transgenic field sites in Syracuse, NY.

We searched interview transcripts and field notes for comments and stories that revealed barriers to future-oriented practice and those that reflected the ways in which TACF and the team at SUNY-ESF have incorporated the dimensions of anticipatory governance into their work. To be clear, TACF and the team at SUNY-ESF have not intentionally used the framework of anticipatory governance; rather, they have incorporated its dimensions -- foresight, engagement, and integration -- into their work to varying degrees as they have managed the limitations of their small staff sizes and sought to generate the knowledge needed to pursue their long-term restoration vision. To us, this unintentional uptake further demonstrates the coherence between the framework of anticipatory governance and conservation practice. In what follows, we describe three key constraints on future-oriented conservation practice, distilled from our interviews and ethnographic field work with scientists involved in American chestnut restoration. These constraints include commitments to a particular vision of the past; practical limitations of time, resources, and expertise; and the policy processes triggered -- or not -- by this restoration project. We then describe how dialogues with public audiences, particularly indigenous communities, and collaborations with citizen scientists and other experts have provided TACF and the team at SUNY-ESF with insight into dimensions of their work that they could not have otherwise anticipated. While these practices are anticipatory in nature and embody some level of foresight, engagement, and integration, they are admittedly incomplete; however, both their accomplishments and their limitations provide lessons about the potential of anticipatory governance for conservation practice.

Constraints on future-oriented conservation practice

Particular pasts

Like most other conservation projects, efforts to introduce blight-resistant American chestnut trees to forests of the eastern United States are concerned with the restoration of specific historical conditions, and as in other projects, those baseline conditions are neither straightforward nor uncontested.

TACF maintains as its mission the return of American chestnut to its native range and former niche in Appalachian forests of the United States (TACF, 2017), and the American Chestnut Research and Restoration Project at SUNY-ESF likewise aims to reintroduce blight-resistant trees throughout the eastern United States, beginning in New York (SUNY-ESF, 2018). Although the difficulty of selecting appropriate baselines is widely discussed in restoration ecology, little attention is given to the reference point for chestnut restoration. Because the demise of American chestnut is singularly attributed to the introduction of *C. parasitica*, restoration efforts are oriented towards the recreation of pre-blight conditions. However, while these efforts are framed in terms of ecological restoration, very little is known about the pre-blight ecology of wild American chestnut (Freinkel, 2007; Paillet, 2002); further, some of the narratives that have supported its ecological importance have recently been challenged. While known to have been structurally important due to its abundance and growth form (Elliott & Swank, 2008), recent analyses indicate that common descriptions of the size of American chestnut trees (Collins et al., 2018) and the species' foundational status in forest ecosystems of the eastern United States (Hanberry & Nowacki, 2016) may reflect exaggerated or erroneous records (Thomas-Van Gundy & Whetsell, 2016a). Its importance as a resource for wildlife is also uncertain. A number of species of Lepidoptera are believed to have been specialists of American chestnut and to have experienced co-extinction with the loss of the species; however, two of these moth species were subsequently found (Opler, 1978). Returning populations of American chestnut to Appalachian forests would likely provide a more abundant and consistent nut mast than is currently provided by oaks and other nut-bearing species, but one of the most voracious consumers of American chestnut, the passenger pigeon, is no longer extant. In general, forests rebounded after the loss of American chestnut, and in fact are more diverse in some locations in the absence of such a dominant and competitive species (Elliott & Swank 2008).

Consequently, a long-term view of the role of American chestnut can be risky for conservation efforts that are dedicated to a particular vision of the species. Looking to the past reveals that American chestnut was not always a part of the American landscape and that its dominance was in many ways the byproduct of anthropogenic modification of forests. Looking to the future draws attention to impending

climate change and the potential for the range of suitable habitat for American chestnut to shift substantially northward, meaning that restoration as currently imagined by TACF and the team at SUNY-ESF may not be feasible in the long-term (see Chapter 2). As TACF's Director of Science said, "I think the challenge is to present an optimistic view of the future without being misleading, sugar-coating something...to present an accurate picture and still keep people excited about it" (Jared Westbrook, TACF Director of Science, personal communication, February 22, 2017). Some scientists involved in American chestnut restoration thus draw more heavily on the importance of the species in Appalachian culture and subsistence as the driving motivation for such a long-term restoration project:

I think the most enduring [reason for restoring chestnut], the one that can capture the imaginations of most people, is this notion of restoring an important part of the American heritage...If chestnut, instead of being native to Appalachians, had been native to upper midwest, we wouldn't be talking about it. The nostalgic, romantic appeal of the whole thing has to do with its connection to the Appalachian culture, which really has a hold on the American imagination...It's not just a species, but a species that is deeply rooted in an important part of the culture. (Kim Steiner, TACF Senior Science Advisor, personal communication, May 11, 2017)

Reliant as TACF is on the support and involvement of public audiences, the success of their restoration efforts rely on continuity with the narrative of American chestnut's historical ecological and cultural importance. However, entrenched commitment to a particular vision of the past undermines the capacity of those involved in this effort to set realistic targets for restoration (Thomas-Van Gundy & Whetsell, 2016b) and to re-evaluate them as the cultural and ecological significance of the species inevitably wane.

Pragmatic priorities

Conversations with scientists involved in American chestnut restoration consistently revealed the ways in which their attention is constrained by the practical need to prioritize expenditures of time and resources among many competing efforts. In practice, conservation funds are limited, and scientists can only focus on so many things at a time; in long-term projects like American chestnut restoration, they must deal with the most immediate considerations first. For TACF and Powell, the priority is the

production of blight-resistant germplasm. Anticipating the future, including the ways in which a resurrected American chestnut might interact with other organisms or the potential impacts of climate change on the development and distribution of the species, are considered secondary concerns. A former TACF Regional Science Director said, “I think people think about [climate change], but nobody has really attempted to address it... We've been so challenged by the big issues of resistance to pathogens that minor or lesser or looming threats such as climate change haven't been a big focus of research” (personal communication, March 16, 2017). TACF’s Director of Science emphasized a similarly short-sighted focus on blight-resistance; attention to how fast blight-resistant American chestnut might be expected to disperse in forests is of lesser concern than the urgency of developing blight-resistant germplasm:

That’s very long-term thinking. We've been so focused on getting these blight-resistant trees that that level of thinking is not one -- that realm of thinking -- that I'm regularly, every day, in that frame of mind... I think the organization is going to transition toward that way of thinking a lot more in the next 5-10 years really, when we have completed the selections at Meadowview, when the transgenic tree is hopefully released, then we'll start thinking more on those terms. [We have] talked about hiring a restoration ecologist, someone that is going to help us think that way. (Jared Westbrook, TACF Director of Science, personal communication, February 22, 2017)

When asked how he decides which concerns about the ecological and environmental impacts of transgenic American chestnut to investigate, Powell said, “How do you choose which ones? I mean, you could test everything, but you don't have the money or the time, so you try to choose what you think is the most significant” (William Powell, personal communication, May 9, 2017).

The triage approach of conservation can also inspire a sense of crisis and urgency that undermine anticipation. When asked about what risks he associated with the large-scale release of transgenic American chestnut trees, one TACF scientist said, “The risk if we had a genetically-resistant American chestnut and were able to get it into the ecosystem? I don't really see a risk, because I think there are so many other screwy things going on out there,” (Kim Steiner, TACF Senior Science Advisor, personal communication, May 11, 2017) referring to the invasion of forests by nonnative plant species, sometimes

to the extent that it constitutes a new forest type, as well as the ongoing loss of ash trees to emerald ash borer and hemlock decline due to woolly adelgid infestation. “So do I see a risk to putting a native species back in? No. Let's put it in context with everything else that's going on around here” (Kim Steiner, TACF Senior Science Advisor, personal communication, May 11, 2017). This crisis narrative has characterized both biodiversity conservation (Soulé, 1985) and biotechnology development (Bud, 1998) since their establishment, and in both cases has promulgated a sense of urgency that justifies taking action without full consideration of ecological and social risks.

Policy problems

The policies designed to govern genetically engineered agricultural crops also shape the kinds of questions that scientists ask about the possible future of blight-resistant American chestnut trees. Significant constraints on anticipation emerge from the fact that the laws that undergird biotechnology regulation in the United States were not designed to consider the ramifications of the wild release of genetically engineered organisms. In fact, they were not designed for the products of biotechnology at all, but have been only uncomfortably extended to agricultural crops in bounded environments. The transgenic trees developed by researchers at SUNY-ESF will be subject to the Coordinated Framework for Regulation of Biotechnology, under which three agencies -- the United States Department of Agriculture (USDA), the Environmental Protection Agency (EPA), and the Food and Drug Administration (FDA) -- draw on existing statutes to govern products of genetic engineering. The insertion of the oxalate oxidase gene was achieved using the now-standard genetic engineering technique in which *Agrobacterium tumefaciens*, a bacterium that causes crown gall disease in plants by incorporating a small segment of its own DNA into a chromosome of its host, is co-opted as a vehicle for the insertion of desired genetic material into plant and animal genomes. This method of gene transfer triggers the regulatory authority of the USDA, which is based on the Plant Protection Act and the novel incorporation of a known or potential plant pest (Kokotovich and Kuzma, 2014). Although principally imagined as an ecological project, transgenic American chestnut trees will produce edible nuts that may be eaten by humans and wildlife. The team at SUNY-ESF has thus also prepared to go through the FDA's

voluntary premarket consultation process, which is intended to ensure the safety of foods developed for human and animal consumption. Whether or not the EPA will exercise oversight over these trees remains unclear. The EPA garners its authority in this case from the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) and has indicated that it would regulate the oxalate oxidase enzyme in American chestnut as a fungicide. However, because oxalate oxidase does not kill or otherwise harm *C. parasitica*, only degrades its oxalic acid into other, less harmful chemicals, this stance is contestable and the topic of ongoing discussions between SUNY-ESF, TACF, and the EPA.

Policy constraints also limit the ability of scientists to empirically investigate the long-term impacts of genetically engineered organisms, particularly trees, in the environment (Strauss, 2009). Multiple scientists interviewed mentioned the limitations that are placed on testing the performance and ecological interactions of transgenic American chestnut on a large scale. One scientist at SUNY-ESF said “We’re just practically thinking about the few years timescale of regulatory [review] because that’s what needs to happen before anything else can happen as far as transgenic [approaches], even further testing” (Andy Newhouse, personal communication, May 9, 2017). In the meantime, all transgenic trees must be prevented from releasing their pollen in the environment; many trees in SUNY-ESF’s field sites are cut down before reaching reproductive maturity, and the rest are bagged to prevent the dispersal of transgenic pollen by wind, insects, or other wildlife. Interestingly, in a context of uncertainty about the reproductive biology of American chestnut, specifically its propensity for long-distance pollen dispersal, regulators and the SUNY-ESF team have largely relied on the expertise of chestnut growers to set permit standards related to the risk of unintended pollination of wild or cultivated chestnut with transgenic pollen. “[B]ased on a little bit of literature and many anecdotal reports from growers,” the USDA has determined that transgenic American chestnut cannot be allowed to flower or produce pollen if sexually compatible species are within 400 meters of their test plots (Andy Newhouse, personal communication, May 9, 2017).

Legal scholars have recently begun to explain how efforts to introduce genetically manipulated organisms, especially proxies of extinct species, into natural environments (IUCN, 2016) might also be

governed by national (Carlin, Worman, & Zakim, 2014) and international (Okuno, 2016) laws regarding endangered and non-native species. However, American chestnut does not meet many of the definitions that are central to those statutes (Camacho, 2015). Due to the large number of stump sprouts that still persist throughout the native range of the species (Dalglish et al., 2015), American chestnut is not considered a federally endangered species, so it is not subject to the provisions of the Endangered Species Act or other policies that might regulate the release of blight-resistant individuals. As a consequence, the hybrid backcross trees developed by TACF will not be subject to federal oversight of any kind, aside from specific prohibitions against the use of non-indigenous plant materials within the boundaries of national parks. While regulatory requirements have in some ways limited the imperative to consider longer-term impacts of transgenic American chestnut, a *lack* of federal oversight has limited TACF's investigation of the kinds of questions being asked about the future impacts of transgenic American chestnut trees. Powell often notes that hybrid trees carry more introduced genetic material and thus, more uncertainty in ecological, dietary, and environmental impacts, than transgenic trees (e.g. Powell, 2014), and laments their exclusion from oversight: "The whole principle here is that we [by introducing a transgenic tree] are going to have less of an environmental impact than the hybrids are, but we're doing a lot of tests that they're not doing, so I think we're doing our due diligence" (William Powell, personal communication, May 9, 2017).

Other scientists interviewed also invoked the notion of "due diligence" to express their confidence in the ability of existing regulatory structures to anticipate the possible negative impacts of the environmental release of a transgenic American chestnut. A former TACF Regional Science Director said, "As long as the regulatory process is carried out with due diligence, I don't have major concerns as far as, ecologically, the dispersal of the transgenic chestnut in the southern Appalachians" (personal communication, March 16, 2017). However, some scholars have described the general inability of the U.S. system for biotechnology regulation to anticipate and accommodate new technoscience (Kuzma et al., 2009), and there is growing attention to specific gaps in oversight for emerging genetic technologies (Kuzma & Tanji, 2010).

Expanding anticipatory capacity with ensembles of foresight, engagement, and integration

The ability of researchers involved in American chestnut restoration to consider the long-term implications of their efforts has been limited by their commitments to specific visions of the cultural and ecological importance of American chestnut in history; by limitations in time and resources and the consequent adoption of a triage approach that justifies acting quickly; and by the nature of biotechnology policy in the United States, which focuses on containment in ways that are incoherent for the restoration of a wild species. Although TACF and the team at SUNY-ESF have never intentionally adopted the framework of anticipatory governance, they have participated in activities that represent an ensemble of foresight, engagement, and integration and have significantly shaped the future of their work.

Engagement with public audiences and social scientists through dialogues and collaborations with citizen scientists, university researchers, and other experts have helped orient scientists involved in American chestnut restoration towards an expanded set of social and ecological considerations associated with their work.

Dialogues

Scientists affiliated with TACF and the American Chestnut Research and Restoration Project at SUNY-ESF routinely engage in public communication, giving talks at garden clubs, libraries, and other community centers. Arguably motivated by an interest in smoothing public perception, especially of a transgenic approach to restoration, some of these interactions have been more substantial and have generated insights that have changed the way scientists think about their work. In May 2017, members of the research team at SUNY-ESF engaged with indigenous representatives at an annual U.S. EPA - Region 2 Indian Nation Leaders Meeting. The meeting included representatives from eight federally recognized tribes within the state of New York, many of which are incorporated into the Iroquois, or Haudenosaunee, Confederacy and are members of the Haudenosaunee Environmental Task Force. Powell presented on his lab's work at the meeting and then participated in break-out sessions that involved him and his colleagues in dialogue with Indian leaders about American chestnut, transgenic trees, and ecological restoration more broadly. Powell had hoped that the meeting would unearth stories about historical uses of American

chestnut by the Haudenosaunee. Although American chestnut was actively cultivated by Native American groups in New York State (Tulowiecki & Larsen, 2015) and used in traditional medicine, meeting participants had few stories to share; lived experience with the tree is rare or nonexistent and inherited memories of it are fading.

However, this restoration project and Powell's participation in the meeting has renewed attention to the culture that once existed around American chestnut and opened opportunities for the re-establishment of relationships between the Haudenosaunee and this species. Prompted by a discussion about the ways in which efforts to restore American chestnut could benefit the Haudenosaunee community, on the second day of the meeting, Powell delivered pure American chestnut seeds to the group. Although these trees will likely succumb to blight before bearing nuts, the exchange allows a new generation of Haudenosaunee to cultivate American chestnut and may facilitate reciprocal restoration (Barnhill-Dilling, 2018). Because no Iroquois words currently exist to describe a genetically engineered organism, particularly a forest tree, Powell's work and his engagement with the Haudenosaunee community may also encourage the development of new language and new relationships as the community decides how a transgenic American chestnut fits into their worldview on the role of humans in caring for, restoring, and shaping the natural world (Patterson, 2018). In other words, biocultural restoration could also facilitate biocultural evolution.

While a number of Indian Nation leaders commended Powell for participating in dialogues with them before releasing his trees, others were more critical of his timing because the transgenic American chestnut has already been developed in a certain way, for a certain purpose, and they see little room for changes in technological design at this point. One participant expressed the need to involve people much earlier in the scientific process, at the idea stage, when decisions are first being made about which trees to modify and why. Group conversations revealed that the Haudenosaunee may have chosen to apply genetic technologies to species that remain culturally important or to those that have been threatened by disease or pests in their parent's lifetimes. Elm trees, which are used in the construction of Iroquois longhouses; ash trees, which are used to make baskets; or trees, like butternut, that are still collected for

food would have been more culturally relevant, but also potentially more fraught. One meeting participant criticized Powell's project as environmental hedonics, pursued just because it could be done even though no one alive today has a relationship with the species as it once was. They pushed Powell to consider the implications of his work "for our children's children" and for others in his field, challenging him to consider how his research might precipitate consequences beyond his intentions. One participant said, "It's not you, it's the process that you represent... We engineered the atom bomb, but should we have used it?"

Perhaps most revelatory of the value of engagement for future-oriented conservation practice, this dialogue with Indian Nation leaders identified a number of concerns about the future of American chestnut that Powell could not have anticipated from his own cultural and professional position. Meeting participants wondered whether an engineered American chestnut would be able to carry out its duties as a plant and whether the chestnut blight fungus would be "happy." One of Powell's graduate students had a similar experience in a workshop he attended on the use of emerging genetic technologies to manipulate natural environments or species. At the workshop, he talked at length with an indigenous law student who drew his attention to *Cryphonectria parasitica* as more than chestnut blight, but as a fungal species with inherent value. Recounting their conversation, he said,

[T]he whole conversation was a big lightbulb for me, thinking about the value of the blight fungus... I would have never even considered that, but, that's something worth thinking about... That was a great example for me of some of the stuff I had been reading about different kinds of expertise and values... and a great example of an effective dialogue where both of us came into it with an open enough mind and both of us left with a slightly changed mind. I loved the opportunity to even have that conversation and to learn from that. (Andy Newhouse, personal communication, May 9, 2017)

Interacting with indigenous groups and individuals has exposed SUNY-ESF researchers to societal dimensions of their work that lie well beyond the technical details that are their focus in the laboratory

and field. These dialogues have also illuminated ways in which American chestnut restoration might be pursued for its future value rather than solely a reconstructions of its historical value.

Collaborations

Many scientists involved in American chestnut restoration are quick to identify the limits of their own expertise, routinely delimiting their own work from other fields; ecologists insist that they are not social scientists, geneticists insist that they are not ecologists, and restorationists insist that they are not geneticists. When asked what successful restoration of American chestnut looks like, Powell said,

I'm going to turn that over to ecologists; my specialty is in plant pathology and molecular biology, and I really need to rely on the expertise of others in my department, school, and others at other universities to do that type of thing, so I really like to turn that over. My goal here at ESF is, once we get through the regulatory process, and light the spark of restoration, turn it over to the ecologists and silviculturalists and the people, and let's -- us -- go back and start working on the next tree... That's where my expertise is, and that's where I should be working. (William Powell, personal communication, May 9, 2017)

Powell's statement reveals both acknowledgement of the limitations of his own knowledge and willingness to turn to other experts when those limits are reached. The integration of collaborators with other kinds of expertise has opened up the anticipations of the SUNY-ESF team beyond what is strictly required for federal approval of their transgenic trees. In an interview, Powell said, "We have our normal bunch of tests that regulators typically ask you do, because they're looking at crops. We want to make sure we're not putting any allergen into the plant. We're looking at nutrition and nontarget species and stuff like that. But since we're looking at a tree, we're actually adding a few extra things" (personal communication, May 9, 2017). In addition to what is required by the USDA, FDA, and EPA, Powell's team has investigated the decomposition of transgenic leaf litter; the impacts of transgenic leaf litter on wood frogs; the impacts of transgenic pollen on bumblebees; and differences in the mycorrhizal associations of transgenic, hybrid, and pure American chestnut trees. Many of these "extra things" have been suggested by other scientists at SUNY-ESF or by members of the public with whom Powell has

interacted via social media or at the many public talks he gives each year. While engagement and integration have expanded the ways in which Powell considers the future impacts of his research, it is important to note that the extra experiments conducted by his team as they prepare for regulatory review are still largely limited to the same kinds of scientific and ecological risks codified in the Coordinated Framework. Powell's team has not considered biogeographic or evolutionary dimensions of chestnut restoration or considered social or cultural risks in detail, and this may be at least partly attributable to the fact that they have not yet formally collaborated with social scientists.

Collaborations, particularly with university researchers and natural resource agencies such as the USDA Forest Service, have been fundamental to the success of TACF as well, both in progress made in the breeding program and in the characterization of emerging challenges for restoration. TACF's Director of Restoration explained:

We're such a small staff. We do some research, but it is not our bread and butter. What I love about TACF, and why I think this model is and can continue to be successful, is that you have an organization that looks long-term versus say a lab at a university or a governmental institution where they have finite resources and timelines. Especially labs at universities, they come and go with the whim of the professor, so to have an overarching organization that has that long-term vision and can keep it going from place to place. Well, this professor retired, let's move that research over here to someone else that might be interested, and try to keep that going. (Sara Fitzsimmons, TACF Director of Restoration, personal communication, May 11, 2017).

Other studies have revealed that building anticipatory governance is challenging when “many actors are willing to work on the issues, but there are few incentives for sharing and building toward a common vision” (Boyd et al., 2015, p. S158). In this case, the organizing mission of American chestnut restoration and the institution of TACF have provided the incentive and infrastructure for collaboration among natural scientists exploring disparate dimensions of American chestnut ecology, genetics, and silviculture.

From the earliest forest surveys for diseased trees in the early 1900s to contemporary breeding efforts, interested public groups have also contributed knowledge, labor, and financial and material

resources to preventing the extinction of American chestnut (Collins, 2016). Since its establishment, TACF has also enrolled non-experts in the scientific work of identifying, breeding, and growing a threatened tree species on a scale that is perhaps unprecedented (Steiner et al., 2017). Scientists involved in the project have suggested that “[c]onsidering the scope, complexity, and duration (20+ years) of [these] breeding projects, this application of citizen science and volunteer labor to the restoration of a species is exceptional and perhaps unique among conservation programs”; they also suggest that it is transferable to other long-term tree conservation projects (Steiner et al., 2017). This engagement of public audiences provides much more than labor and has generated both an understanding of the fitness of blight-resistant germplasm being developed in Meadowview, Virginia for regional conditions as well as locally adapted germplasm (Steiner et al., 2017).

Public engagement in the project via forms of citizen science have also significantly influenced the direction of TACF’s research, with implications for its long-term success. For most of its tenure, TACF had been exclusively focused on breeding American chestnut trees for resistance to chestnut blight. However, another introduced pathogen, *Phytophthora cinnamomi*, predated the arrival of *C. parasitica* in the United States and is responsible for the permanent contraction of the range of American chestnut, eliminating populations throughout the warmer and wetter Coastal Plain of Georgia, North Carolina, and other states in the late 1800s. In 2004, all of the American chestnut trees planted by Dr. Joe James, a retired physician, on his farm in South Carolina died within three years of planting, and not from chestnut blight infection. Dr. Steve Jeffers at Clemson University identified the culprit as *P. cinnamomi* and James began what would become a Foundation-wide initiative on breeding for resistance to *Phytophthora*. James and others have now tested the existing breeding stock of TACF for *Phytophthora* resistance and discovered that some of TACF’s backcross lines retained this trait from their Chinese parents. According to TACF’s Director of Restoration, the national organization “didn't even recognize it as an issue until [he] started having it...It wasn't something that was necessarily predictable, but he brought it to the forefront... Is this a Foundation-wide problem? Now? No. Will it be? Probably.” (Sara Fitzsimmons, personal communication, May 11, 2017).

Conclusion

The case of American chestnut restoration demonstrates that there are substantial philosophical, practical, and political barriers to the ability of scientists and conservationists to consider the broad and long-term implications of their work. However, it also shows that these constraints can be partially overcome when diverse public audiences and experts from across disciplines are engaged, with scientists, in activities that draw attention to the possible futures of a given technology or intervention. In this case, a philosophical commitment to the restoration of American chestnut to a particular, but problematic, reference point has undermined the willingness of scientists involved in this project to look to the future and anticipate long-term changes in the ecological and cultural relevance of the species. Dialogues with indigenous stakeholders have renewed attention to American chestnut restoration as a biopolitical undertaking in which values-based decisions are made about which species to save and why (Biermann and Anderson, 2017). These dialogues have also identified the potential for American chestnut restoration, insofar as it opens opportunities for biocultural restoration, to have meaning that is both future-oriented and restorative. Future-oriented or anticipatory conservation of American chestnut is also constrained by practical limits on the time and resources available to the relatively small and non-profit organizations that are spearheading this restoration effort. The enrollment of citizen scientists and collaborations with university researchers have vastly expanded the ability of TACF, in particular, to think beyond blight-resistance and incorporate other ecological complexities, including other pathogens and regional climates, into their breeding program. Finally, the application of biotechnology policies developed for contained agricultural systems to transgenic American chestnut trees and the primacy of regulatory approval have shaped the kinds of questions currently being asked -- or not -- about the biological, ecological, and social future of these trees. Again, however, engagement with public audiences and other experts has prompted researchers at SUNY-ESF to consider questions that uniquely apply to wild, forest species, and to think about their research -- including the tree they are modifying, the fungus they are attenuating, and the scientific field they are shaping -- in new ways.

The implementation of anticipatory governance in this case is both unintentional and incomplete, and much more could be done to enact ensembles of foresight, engagement, and integration in this and other conservation contexts. However, the details of American chestnut restoration nevertheless demonstrate the potential of upstream, democratic engagement to improve both the science and social sensitivity of a conservation project. The framework of anticipatory governance is well equipped for decision-making in the Anthropocene, as its uncertainty, complexity, and novelty increasingly prompt both the reorientation of conservation science towards the future and the adoption of technologically intensive approaches to the protection of biodiversity.

References

- Adams V, Murphy M and Clarke AE (2009) Anticipation: Technoscience, life, affect, temporality. *Subjectivity* 28(1): 246–265. DOI: 10.1057/sub.2009.18.
- Armitage D, Berkes F, and Doubleday N (eds) (2007) *Adaptive Co-management: Collaboration, learning and multi-level governance*. Vancouver: UBC Press.
- Barben D, Fisher E, Selin C and Guston DH (2008) Anticipatory governance of nanotechnology: Foresight, engagement, and integration. In: Hackett EJ, Amsterdamska O, Lynch M and Wajcman J (eds) *The Handbook of Science and Technology Studies*. Cambridge, MA: The MIT Press, 979–1000.
- Barnhill-Dilling SK (2018) Dissertation: *Engineered Governance: Public Engagement as a Path to Inclusive Environmental Governance in Genetically Engineered Trees*. Department of Forestry and Environmental Resources. North Carolina State University. Raleigh, NC. Available online: <https://repository.lib.ncsu.edu/handle/1840.20/35317>
- Bennett NJ, Roth R, Klain SC, Chan K, Christie P, Clark DA, ... Wyborn C (2017) Conservation social science: Understanding and integrating human dimensions to improve conservation. *Biological Conservation*, 205, 93–108. <https://doi.org/10.1016/j.biocon.2016.10.006>
- Biermann C and Anderson RM (2017) Conservation, biopolitics, and the governance of life and death. *Geography Compass* 11(10): e12329. DOI: 10.1111/gec3.12329.
- Boivin NL, Zeder MA, Fuller DQ, Crowther A, Larson G, Erlandson JM, ... and Petraglia MD (2016) Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. *Proceedings of the National Academy of Sciences* 113(23), 6388-6396.
- Boyd E, Nykvist B, Borgström S, and Stacewicz IA (2015) Anticipatory governance for social-ecological resilience. *AMBIO* 44(S1), 149–161. <https://doi.org/10.1007/s13280-014-0604-x>
- Buck HJ (2015) On the possibilities of a charming Anthropocene. *Annals of the Association of American Geographers* 105(2): 369–377.
- Bud R (1998) Molecular biology and the long-term history of biotechnology. In: Thackray A (ed.) *Private Science: Biotechnology and the Rise of the Molecular Sciences*. Philadelphia: University of Pennsylvania Press, 3-19.
- Camacho AE (2015) Going the Way of the Dodo: De-Extinction, Dualisms, and Reframing Conservation. *Washington University Law Review* 92(4): 849–906.
- Carlin NF, Wurman I and Zakim T (2014) How to permit your mammoth: Some legal implications of de-extinction. *Stanford Environmental Law Journal* 33(1): 3-58.
- Choi YD (2007) Restoration ecology to the future: a call for new paradigm. *Restoration Ecology* 15(2): 351–353. DOI: 10.1111/j.1526-100X.2007.00224.x

- Civil Society Working Group on Gene Drives (2018) A Call for Conservation with a Conscience: No Place for Gene Drives in Conservation. Available at: http://www.synbiowatch.org/wp-content/uploads/2016/09/letter_vs_genedrives.pdf (April 7, 2018)
- Collins K (2016) Power to the people: Citizen science moves TACF's mission forward. *Chestnut* 30(2): 32-35.
- Collins RJ, Copenheaver CA, Kester ME, et al. (2018) American Chestnut: Re-Examining the Historical Attributes of a Lost Tree. *Journal of Forestry* 116(1): 68-75. DOI: 10.5849/JOF-2016-014.
- Cook CN, Inayatullah S, Burgman MA, et al. (2014) Strategic foresight: how planning for the unpredictable can improve environmental decision-making. *Trends in Ecology & Evolution* 29(9): 531–541. DOI: 10.1016/j.tree.2014.07.005.
- Corlett RT (2016a) Restoration, Reintroduction, and Rewilding in a Changing World. *Trends in Ecology & Evolution* 31(6): 453–462. DOI: 10.1016/j.tree.2016.02.017.
- Corlett RT (2016b) A Bigger Toolbox: Biotechnology in Biodiversity Conservation. *Trends in Biotechnology*. DOI: 10.1016/j.tibtech.2016.06.009.
- Dalgleish H, Nelson C, Scrivani J, et al. (2015) Consequences of Shifts in Abundance and Distribution of American Chestnut for Restoration of a Foundation Forest Tree. *Forests* 7(1): 4. DOI: 10.3390/f7010004.
- Elliott KJ and Swank WT (2008) Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*). *Plant Ecology* 197(2): 155–172. DOI: 10.1007/s11258-007-9352-3.
- Fisher E, Mahajan RL and Mitcham C (2006) Midstream Modulation of Technology: Governance From Within. *Bulletin of Science, Technology & Society* 26(6): 485–496. DOI: 10.1177/0270467606295402.
- Fisher E and Schuurbiens D (2013) Socio-technical Integration Research: Collaborative Inquiry at the Midstream of Research and Development. In: Doorn N., Schuurbiens D., van de Poel I., Gorman M. (eds) *Early engagement and new technologies: Opening up the laboratory. Philosophy of Engineering and Technology, vol 16*. Springer, Dordrecht.
- Freinkel S (2007) *American chestnut: the life, death, and rebirth of a perfect tree*. Berkeley: University of California Press.
- Fuerth LS (2009) Foresight and anticipatory governance. *Foresight*, 11(4), 14-32. DOI: 10.1108/14636680910982412
- Gravatt F (1949) Chestnut blight in Asia and North America. *Unasylva* 3: 2–7.
- Gunderson L and Light SS (2007) Adaptive management and adaptive governance in the everglades ecosystem. *Policy Sciences* 39(4): 323–334. DOI: 10.1007/s11077-006-9027-2.
- Guston D (2012) The pumpkin or the tiger? Michael Polanyi, Frederick Soddy, and anticipating emerging technologies. *Minerva*, 50, 363–379.

- Guston DH (2014) Understanding ‘anticipatory governance.’ *Social Studies of Science*, 44(2), 218–242.
- Hanberry BB and Nowacki GJ (2016) Oaks were the historical foundation genus of the east-central United States. *Quaternary Science Reviews*, 145, 94–103. DOI: 10.1016/j.quascirev.2016.05.037
- Hobbs RJ, Hallett LM, Ehrlich PR, et al. (2011) Intervention Ecology: Applying Ecological Science in the Twenty-first Century. *BioScience* 61(6): 442–450. DOI: 10.1525/bio.2011.61.6.6.
- Huang H, Dane F and Kubisiak T (1998) Allozyme and RAPD analysis of the genetic diversity and geographic variation in wild populations of the American chestnut (Fagaceae). *American Journal of Botany* 85(7): 1013–1013.
- IUCN (2016) IUCN Species Survival Commission Guiding Principles on Creating Proxies of Extinct Species for Conservation Benefit. Gland, Switzerland: IUCN Species Survival Commission.
- Jacobs DF, Dalglish HJ and Nelson CD (2013) A conceptual framework for restoration of threatened plants: the effective model of American chestnut (*Castanea dentata*) reintroduction. *New Phytologist* 197(2): 378–393. DOI: 10.1111/nph.12020.
- Johnson JA, Altwegg R, Evans DM, Ewen JG, Gordon IJ, Pettoelli N, and Young JK (2016) Is there a future for genome-editing technologies in conservation? *Animal Conservation*, 19(2), 97–101.
- Jolibert C and Wesselink A (2012) Research impacts and impact on research in biodiversity conservation: The influence of stakeholder engagement. *Environmental Science & Policy* 22: 100–111. DOI: 10.1016/j.envsci.2012.06.012.
- Kareiva P, Marvier M, Lalasz R (2012) Conservation in the Anthropocene: beyond solitude and fragility. *Breakthrough Journal* 2. Available at: <https://thebreakthrough.org/index.php/journal/past-issues/issue-2/conservation-in-the-anthropocene> (April 10, 2018)
- Kareiva P and Fuller E (2016) Beyond Resilience: How to Better Prepare for the Profound Disruption of the Anthropocene. *Global Policy* 7: 107–118. DOI: 10.1111/1758-5899.12330.
- Karinen R and Guston DH (2009) Toward Anticipatory Governance: The Experience with Nanotechnology. In: Kaiser M, Kurath M, Maasen S, et al. (eds) *Governing Future Technologies*. Dordrecht: Springer Netherlands, pp. 217–232. DOI: 10.1007/978-90-481-2834-1_12.
- Kass GS, Shaw RF, Tew T, et al. (2011) Securing the future of the natural environment: using scenarios to anticipate challenges to biodiversity, landscapes and public engagement with nature: Scenarios and the natural environment. *Journal of Applied Ecology* 48(6): 1518–1526. DOI: 10.1111/j.1365-2664.2011.02055.x.
- Kearnes MB, Macnaghten PM, and Wilsdon J (2006) *Governing at the nanoscale: people, policies and emerging technologies*. London: Demos.
- Kokotovich A and Kuzma J (2014) Conflicting futures: Environmental regulation of plant targeted genetic modification. *Bulletin of Science, Technology & Society* 34(3–4): 108–120.
- Kumar S (2012) Extinction need not be forever. *Nature News* 492(7427): 9.

- Kuzma J, Najmaie P and Larson J (2009) Evaluating oversight systems for emerging technologies: a case study of genetically engineered organisms. *The Journal of Law, Medicine & Ethics* 37(4): 546–586.
- Kuzma J and Tanji T (2010) Unpackaging synthetic biology: Identification of oversight policy problems and options: Oversight policy for synthetic biology. *Regulation & Governance* 4(1): 92–112. DOI: 10.1111/j.1748-5991.2010.01071.x.
- Kareiva P, Marvier M, and Lalasz R (2012) Conservation in the Anthropocene: beyond solitude and fragility. *Breakthrough Journal* 2. Retrieved from <http://thebreakthrough.org/index.php/journal/past-issues/issue-2/conservation-in-the-anthropocene/>.
- Lockwood M, Davidson J, Curtis A, et al. (2010) Governance Principles for Natural Resource Management. *Society & Natural Resources* 23(10): 986–1001. DOI: 10.1080/08941920802178214.
- Marris E (2011) *Rambunctious garden: saving nature in a post-wild world*. Bloomsbury Publishing USA.
- Milgroom MG and Cortesi P (2004) Biological control of chestnut blight with hypovirulence: A critical analysis. *Annual Review of Phytopathology* 42(1): 311–338. DOI: 10.1146/annurev.phyto.42.040803.140325.
- National Academies of Sciences, Engineering, and Medicine (NASEM) (2016) *Gene Drives on the Horizon: Advancing Science, Navigating Uncertainty, and Aligning Research with Public Values*. Washington, DC: The National Academies Press.
- Okuno E (2016) Frankenstein’s Mammoth: Anticipating The Global Legal Framework For De-extinction. *Ecology LQ* 43: 581.
- Opler PA (1978) Insects of American chestnut: possible importance and conservation concern. In: *Proceedings of the American chestnut symposium*. Morgantown, West Virginia: West Virginia University Press, 83-85.
- Paillet FL (2002) Chestnut: history and ecology of a transformed species. *Journal of Biogeography* 29(10–11): 1517–1530.
- Patterson N (2018) Indigenous Perspectives on the Use of Biotechnology in Forests. National Academies of Science, Engineering, and Medicine Webinar. Available at: <http://nas-sites.org/dels/studies/forest-biotech/webinar-indigenous/> (April 19, 2018)
- Peterson G, Cumming G, and Carpenter S (2003) Scenario Planning: A Tool for Conservation in an Uncertain World. *Conservation Biology* 17(2): 358-366.
- Poli R (2014) Anticipation: What about turning the human and social sciences upside down? *Futures* 64: 15–18. DOI: 10.1016/j.futures.2014.10.003.
- Powell W (2014) The American chestnut’s genetic rebirth. *Scientific American* 310(3): 68–73. DOI: 10.1038/scientificamerican0314-68.

- Redford KH, Adams W and Mace GM (2013) Synthetic Biology and Conservation of Nature: Wicked Problems and Wicked Solutions. *PLoS Biology* 11(4): e1001530. DOI: 10.1371/journal.pbio.1001530.
- Sarewitz D (2015) Science can't solve it. *Nature* 522: 414.
- Soulé ME (1985) What is conservation biology? *BioScience* 35(11): 727-34.
- Soulé M (2013) The "New Conservation". *Conservation Biology* 27(5): 895–897. DOI: 10.1111/cobi.12147.
- Steiner KC, Westbrook JW, Hebard FV, Georgi LL, Powell WA, and Fitzsimmons SF (2016) Rescue of American chestnut with extraspecific genes following its destruction by a naturalized pathogen. *New Forests* 48:317-336. DOI: 10.1007/s11056-016-9561-5.
- Sterling EJ, Betley E, Sigouin A, Gomez A, Toomey A, Cullman G, et al. (2017). Assessing the evidence for stakeholder engagement in biodiversity conservation. *Biological Conservation* 209: 159–171. DOI: 10.1016/j.biocon.2017.02.008
- Strauss SH, Tan H, Boerjan W, et al. (2009) Strangled at birth? Forest biotech and the Convention on Biological Diversity. *Nature biotechnology* 27(6): 519–527.
- SUNY-ESF (2018) Restoring the American chestnut. The American Chestnut Research and Restoration Project. Available at: <http://www.esf.edu/chestnut/resistance.htm> (April 2, 2018)
- Taylor HR and Gemmill NJ (2016) Emerging technologies to conserve biodiversity: further opportunities via genomics. Response to Pimm et al. *Trends in ecology & evolution* 31(3): 171-172.
- The American Chestnut Foundation (TACF) (2017) 2017-2027 Strategic Plan. Available at: <https://www.acf.org/wp-content/uploads/2017/09/WEB-Strategic-Plan-090617.pdf?x86657> (April 2, 2018)
- The American Chestnut Foundation (TACF) (2018) About TACF. Available at: <https://www.acf.org/about-us/> (April 2, 2018)
- Thomas MA, Roemer GW, Donlan CJ, et al. (2013) Gene tweaking for conservation. *Nature* 501: 485–486.
- Thomas-Van Gundy M and Whetsell R (2016a) West Virginia's Big Trees: Setting the Record Straight. *Journal of Forestry* 114(5): 582.
- Thomas-Van Gundy M and Whetsell R (2016b) Realistic restoration targets. *Journal of the American Chestnut Foundation* 2(30):28-29.
- Tulowiecki SJ and Larsen CPS (2015) Native American impact on past forest composition inferred from species distribution models, Chautauqua County, New York. *Ecological Monographs* 85(4): 557–581. DOI: 10.1890/14-2259.1.

- van Oppen MJH, Oliver JK, Putnam HM, et al. (2015) Building coral reef resilience through assisted evolution. *Proceedings of the National Academy of Sciences* 112(8): 2307–2313. DOI: 10.1073/pnas.1422301112.
- Vlieg TJ and Zandvoort M. (2013) Reactive versus anticipative adaptive management of deltas: The Sacramento-San Joaquin delta and the Rhine-Meuse delta compared. *Water Governance* 05-06:52-57.
- Whiteley AR, Fitzpatrick SW, Funk WC, et al. (2015) Genetic rescue to the rescue. *Trends in Ecology & Evolution* 30(1): 42–49. DOI: 10.1016/j.tree.2014.10.009.
- Williams M, Zalasiewicz J, Haff PK, Schwägerl C, Barnosky AD, and Ellis EC (2015) The Anthropocene biosphere. *The Anthropocene Review* 2(3): 196–219.
- Winner L (1986) *The whale and the reactor: A search for limits in an age of high technology*. The University of Chicago Press.

CHAPTER 5

TOWARDS THE SOCIAL ENGINEERING OF GENETIC ENGINEERING IN CONSERVATION

Biodiversity conservation has received a great deal of attention from critical scholars, who tend to see its practice as culturally inappropriate and insensitive; short-sighted and narrowly focused; and embedded in political-economic systems that benefit the powerful and dispossess the vulnerable. Conservation and ecological restoration have often been unsuccessful by their own metrics as well, failing to make lasting improvements in the status of threatened species or the integrity of ecosystems. The inclusion of emerging genetic technologies in conservation practice may only exacerbate these critiques, as genetic technoscience has been characterized by its own set of ecological, social, and political shortcomings. While critics continue to call for more attention to the societal dimensions and long-term implications of both technoscience and conservation practice, many well-intentioned scientists, though deeply concerned about the social and ecological consequences of their work, do not know how to integrate critical theories into their scientific practice. The chapters of this dissertation each point to practical, if at times political, ways that concerns about the right of current and future generations to environmental self-determination; meaningful democratic participation in environmental science and governance; and equitable access to environmental resources, especially the genetic commons, might be incorporated into the practice of resurrection science.

The proposed restoration of American chestnut to its former niche and native range in the eastern United States using some combination of transgenic and hybrid trees is currently positioned to be one of the first landscape-scale applications of resurrection science. This dissertation thus uses the specific ecological, technological, and political realities of the American chestnut case to explore this nascent approach to biodiversity conservation in the Anthropocene. *Chapter 2* employs species distribution modeling to consider potential long-term changes in the distribution and quantity of suitable habitat for American chestnut. Though limited in important ways, this model draws attention to the possible ecological consequences of reintroducing blight-resistant American chestnut both within and beyond its

native range and the implications of climate change for restoration practice. Given the potential for American chestnut restoration to create novel ecosystems and to have impacts that transcend national borders, this exercise is essential for the successful and responsible reintroduction of the species. This chapter draws attention to the utility of species distribution modeling as valuable foresight tool in conservation, one that can prompt conservationists to reconsider the purpose and potential impacts of their efforts. *Chapter 3* describes the ways in which scientists involved in American chestnut restoration have successfully circumvented tendencies towards the privatization, commodification, and commercialization of nature that have been associated with the use of genetic technoscience in agricultural contexts. Revealing genetic technologies as flexible in their political consequences, this chapter challenges critical scholars to conduct more nuanced analyses of the various applications of these technologies, rather than assuming their inherent complicity in the neoliberal project. This chapter points to the potential for the anticipations, agency, and normative commitments of scientists, combined with the context of restoration, to resist the genetic commodification of nature. *Chapter 4* explores three barriers to future-oriented practice in American chestnut restoration and the ways in which dialogues with indigenous communities and collaborations with both citizen scientists and other experts have expanded the capacity for scientists to anticipate and prepare for the social and ecological ramifications of their work. This chapter suggests that the framework of anticipatory governance provides a valuable approach to making decisions about the feasibility and desirability of using genetic technologies in species resurrection, especially under the conditions of novelty, uncertainty, and complexity that characterize the Anthropocene.

Most broadly, this dissertation demonstrates the unique ability of deeply interdisciplinary research to paint a comprehensive picture of the geographical, ecological, social, and political dimensions of technoscience. As in the parable of the blind men and the elephant, single disciplinary approaches tend to interpret partial perspectives as full ones. These partial perspectives are often overly simplistic, to the detriment of our ability to understand and appreciate the complexity of socio-environmental systems. As a field and movement, much of conservation has indeed been short-sighted, colonial, and unaware of its

own implicit values; but it has also evolved a great deal in its relatively short history and is increasingly cognizant of the social and ecological externalities of some of its approaches. Addressing the implementation gap between critical social science and applied natural science requires critical theory that does not alienate scientists and science that does not see social and political futures as outside of its purview. This dissertation embodies this kind of translational work as it integrates disciplinary perspectives in order to explore some of the most interesting and difficult questions about conservation in the Anthropocene.