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Transformational restoration: novel ecosystems in Denmark

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ABSTRACT
Restoring the estimated 1 billion hectares of degraded forests must consider future climate accompanied by novel ecosystems. Transformational restoration can play a key role in adaptation to climate change but it is conceptually the most divergent from contemporary approaches favoring native species and natural disturbance regimes. Here, we review concepts of novelty in ecosystems with examples of emergent/neo-native and designed novel ecosystems, with application to transformational restoration. Danish forests have a high degree of novelty and provide a realistic context for discussing assisted migration, one method of transformational adaptation. Deforestation and impacts of past land use created a highly degraded landscape dominated by heathland in western Denmark. Restoration with non-native species began 150 years ago because the native broadleaves could not establish on the heathlands. Danish forestry continues to rely extensively on non-native species. Preparing for transformational adaptation requires risky research today to prepare for events in the future and refugia from the last glaciation may provide genetic material better adapted to future climate. A new project will test whether species and provenances from the Caspian forests in Iran possess greater genetic diversity and superior resistance (physiological adaptability) and resilience (evolutionary adaptability) and possibly a gene pool for future adaptation.

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Introduction

Forest landscape restoration (FLR) has grabbed the international spotlight with the main focus on the Bonn Challenge and regional initiatives. Nations, regions and the private sector have pledged over 150 million hectares of FLR to commence by 2020 (http://www.bonnchallenge.org/). Africa has made the most commitments (Figure 1) and more countries in Latin America have made commitments to the Bonn Challenge than to the regional LAC 20 × 20 initiative (http://www.wri.org/our-work/project/initiative-20x20/restoration-commitments#project-tabs). The FLR movement has been suggested as complementary to other efforts to counter degradation and loss of biodiversity, including the UNCCD goal of land degradation neutrality (http://www.unccd.int/Lists/SiteDocumentLibrary/Rio+20/UNCCD_PolicyBrief_ZeroNetLandDegradation.pdf) and the CBD Aichi 15 target to restore 15% of all degraded ecosystems on Earth by 2020 (https://www.cbd.int/doc/strategic-plan/targets/T15-quick-guide-en.pdf). Many have suggested that the REDD+ efforts under the UNFCCC could produce joint benefits of restoration and carbon sequestration (e.g. Rizvi et al. 2015; Stanturf et al. 2015). The UN Strategic Plan for Forests calls for a target to increase forest area by 3% worldwide by 2030, signifying an increase of 120 million hectares, an area over twice the size of France (https://www.un.org/esa/forests/wp-content/uploads/2016/12/UNSPF_AdvUnedited.pdf).

The Bonn Challenge and related efforts at countering centuries of landscape degradation cannot focus on simply correcting the excesses of the past or by returning ecosystems to historic, pre-industrial states. On-going land use change to meet the needs of an expanding global population and changes in climate and increased frequency of extreme events are projected to lead to novel climates and emergence of novel ecosystems (Williams and Jackson 2007; Williams et al. 2007; Caloiero et al. 2016). Thus, efforts at restoring degraded forests must take into account future climate and provide solutions that are robust under much uncertainty as to the nature of future conditions and adaptive to climate change (Spittlehouse and Stewart 2004; Bolte et al. 2009; Keenan 2015; Stanturf et al. 2015).

FLR is a planned process of restoring ecological integrity and enhancing human livelihood that differs from site-level restoration because it seeks to restore ecological processes that operate at larger landscape-level scales (SER 2004; Stanturf, Palik, Williams, et al. 2014; Mansourian 2017). Some advantages of FLR over ecological restoration include the broad focus on landscape-level restoration and the explicit inclusion of livelihoods and food security needs, rendering FLR more appropriate in the developing world where many opportunities for forest restoration exist in mosaic landscapes (Stanturf 2015). Ecological restoration often is motivated by restoration to a more natural (i.e. pristine) state and then to preserve the restored area (e.g. Stanturf et al. 2001).

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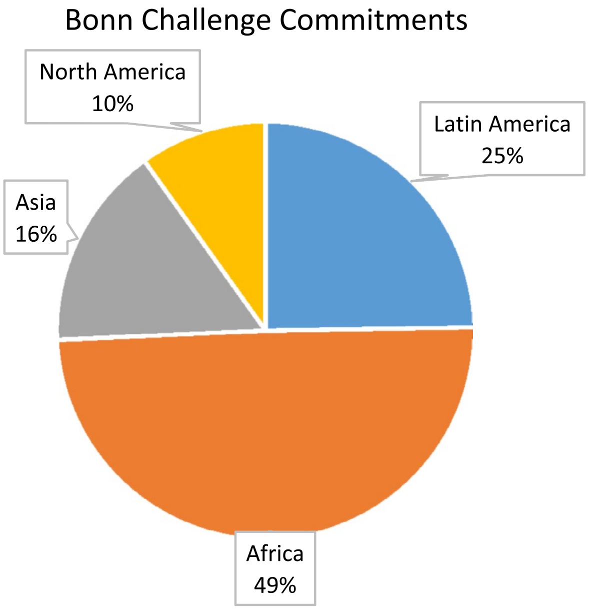

Figure 1. Most of the Bonn Challenge commitments, in terms of hectares pledged for restoration, have been in Africa.

Potential disadvantages of FLR are a possible narrow focus on local perceptions of needs or demands of funding programs rather than broader social needs. For example, restoring degraded forests with REDD + funding would not necessarily include biodiversity concerns (Alexander et al. 2011; Gardner et al. 2012). With respect to the FLR and the Bonn Challenge, Mansourian et al. (2017) questioned whether emphasizing pledges of area restored (i.e. quantity targets), without regard to the quality in terms of functions restored, was not a recipe for "covering vast areas of the world in trees of limited value to local people and biodiversity" (Mansourian et al. 2017, p. 178). Even though an estimated 1 billion to 6 billion hectares of degraded landscapes already exist (Laestadius et al. 2011; Gibbs and Salmon 2015), climate change and business-as-usual land use will add to the need to restore ecosystems. This daunting task can best be addressed at the landscape scale (Menz et al. 2013; Kuuluvainen et al. 2015; Latawiec et al. 2015; Stanturf 2015) and FLR can play a key role in adaptation to climate change (Stanturf et al. 2015).

Climate change adaptation strategies can be characterized as incremental, anticipatory, or transformational (Joyce et al. 2013; Pinkard et al. 2015; Stanturf 2015). The incremental strategy is a no-regrets approach where restoration actions provide benefits under the current climate; but this is not a business-as-usual approach. The anticipatory strategy for adaptation uses the same techniques but is more future-climate oriented, while the transformational strategy takes proactive measures to adapt to future climate conditions. Commonalities among these strategies include favouring genotypes adapted to future conditions (Pedlar et al. 2011; Williams and Dumroese 2013; Dumroese et al. 2015), resisting pathogens (Millar and Stephenson 2015), managing herbivory to ensure adequate regeneration (Rooney and Waller 2003; Côté et al. 2004), encouraging species and structural diversity at stand and landscapes levels (Millar et al. 2007; Santopuoli et al. 2016) and providing connectivity and reducing fragmentation (Stanturf 2015; Stanturf et al. 2015). Here, we explore transformational restoration, an approach based on the most future-oriented adaptation strategy. Even though this strategy seems conceptually the most divergent from contemporary restoration that focuses on native species and natural disturbance regimes (Stanturf, Palik, Dumroese 2014; Stanturf, Palik, Williams, et al. 2014), we posit that foresters already have much experience with novel ecosystems, non-native species and assisted migration. Our objective in this paper is to review concepts of novelty in ecosystems, present examples of emergent/neo-native and designed novel ecosystems and discuss how this applies to transformational restoration practices under global change. To anchor these discussions in a realistic context, we present a case study of Denmark, a country with forests that for historical reasons are comprised of a high degree of novelty.

Transformational restoration – what do we mean?

Three types of transformational adaptations are those that are adopted at a much larger scale, that are truly new to a particular region or resource system and that transform places and shift locations (Kates et al. 2012). Transformational restoration of degraded ecosystems anticipates rapidly changing climate and embraces the novelty of emergent and neo-native ecosystems as well as planned novelty in active restoration (Hobbs et al. 2006, 2011; Sarr and Puettmann 2008). By novelty, we adopt the definition of Radeloff et al. (2015, p. 2051) "… the degree of dissimilarity of a system, measured in one or more dimensions relative to a reference baseline … novelty varies in degree, it is multidimensional, can be measured, and requires a temporal and spatial reference". The three adaptation strategies differ in their tolerance of novelty in the restored ecosystem; while transformational adaptation embraces novelty, incremental adaptation is intolerant of novelty and the anticipatory strategy has intermediate tolerance of novelty. The degree of "novelty-tolerance" can be illustrated by actions regarding novel ecosystems, where incremental adaptation would seek to prevent establishment of non-native species and emergent assemblages of native species in new combinations (neo-native ecosystems); anticipatory adaptation would allow and seek to manage emergent, neo-native assemblages, possibly allowing non-native species with functional equivalencies to maladapted native species; and transformational management would not only manage emergent ecosystems but also truly novel assemblages in which non-native species dominate (Stanturf 2015).

Novel ecosystems will spontaneously arise under land use change and altered climate (Alig et al. 2004; Briske et al. 2015; Martinuzzi et al. 2015). Extreme events present opportunities to transform ecosystems and incorporate more novelty in the near-term but intentional or planned transformation will likely be controversial as it goes against the received wisdom that locally adapted, native species and natural disturbance regimes are best (Leimu and Fischer 2008; Boshier et al. 2015), in the sense of most sustainable. Transformational restoration will create novel ecosystems by moving species far beyond their historical ranges (Pedlar et al. 2012; Lunt et al. 2013; Benito-Garzón and Fernández-Manjarrés 2015); and by purposeful introduction of non-native (Davis et al. 2011) or genetically modified species (Seddon et al. 2014; Potter et al. 2017). Is there a need for such extreme measures? What genetic material to move to where? What experience do we have that suggests factors to consider in future efforts? The following sections will examine these questions in greater detail.

Novel ecosystems

The notion of novel ecosystems as advanced by Hobbs and others (Hobbs et al. 2006, 2013) required anthropogenic intervention (disturbance). If a system could return to its former state if the disturbance was abated, it was a hybrid ecosystem; if it remained in the new state, it was novel (Hobbs et al. 2006, 2013). As stated above, we adopt the broader definition of Radeloff et al. (2015). Thus, novel ecosystems may emerge as an indirect consequence of land use change interacting with ecological factors (an emergent or neo-native ecosystem) or by intentional creation of a new system by introduction of non-native plants. Two examples follow, the Allegheny Hardwoods of north-western Pennsylvania dominated by black cherry (*Prunus serotina* Ehrh.) in the eastern US and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) introduction into Western Europe.

Emergent novelty – Allegheny Hardwoods

The dissected Allegheny Plateau in western and central New York, northern and western Pennsylvania, northern and western West Virginia and eastern Ohio is comprised of a southern unglaciated part and a northern part that was subjected to Wisconsinan glaciation. Prior to European settlement in the late 1700s and early 1800s, the forest was minimally affected by native Americans and mature and over-mature forests covered the plateau with eastern hemlock (*Tsuga canadensis* (L.) Carr.), American beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) being the dominant species (Marquis 1975; Whitney 1990). Black cherry, red maple (*Acer rubrum* L.), white ash (*Fraxinus americana* L.) and birches (*Betula alleghaniensis* Britton and *B. lenta* L.) were common associates, especially in stands developing after windthrow. Small stands of white pine (*Pinus strobus* L.) were exploited first by the European settlers but cutting remained localized, mostly at lower elevations along the major streams until the advent of steam power in the middle of the 1800s.

Tanneries that utilized hemlock bark, band mills to produce lumber, chemical wood factories to produce charcoal and distillates and logging railroads transformed the forests. By 1920, the virgin and partially harvested forest was almost completely clearcut (Marquis 1975). Uncontrolled wildfires in the abundant logging slash had an impact on the species composition of the forests regenerating in the clearcuts, virtually eliminating white pine and confining hemlock to wet riparian areas. Along with the liquidation of the original forest, the native white-tailed deer (*Odocoileus virginianus* Zimmerman) was hunted for meat and locally extirpated by 1890. Restrictions on hunting and introduction of deer from other areas began to rebuild deer herds, aided by the abundant browse in the clearcuts. By the 1920s, deer were so abundant that they were causing significant damage to agricultural crops as well as forest reproduction (Marquis 1975). Deer populations peaked in the 1940s and then declined as browse became limited in the maturing second growth forests (Figure 2). Today, deer populations remain high and create problems for regenerating after timber harvest (deCalesta 1994a; Horsley et al. 2003) and impacts on the forest floor flora (Tilghman 1989) cascade into the fauna (deCalesta 1994b). The trajectories of ecosystem development remain novel, preventing the system from returning to a historical state even if the deer populations were to be reduced (Royo et al. 2010; Kain et al. 2011)

Designed novelty – Douglas-fir

Large-scale reforestation and afforestation programs globally have concentrated on a few genera, principally conifers such as *Pinus* spp. and *Picea* spp. or broadleaves such as *Eucalyptus*

Figure 2. Experiments that use fencing to exclude deer from browsing the understory show their effect on biodiversity and regeneration of woody species. This experiment on the Bradford Ranger District of the Allegheny National Forest in northwest Pennsylvania, USA show the effect of deer browse (on the left) versus native understory (right of photo). (Credit: US Forest Service).

spp. and *Acacia* spp. Often involving intercontinental movement and monoculture plantations, such designed novelty can have adverse social (e.g. Cao et al. 2011; Andersson et al. 2016) and ecological effects (Ledgard 2001; Simberloff et al. 2010; Taylor et al. 2016). Experience with Douglas-fir in Europe has been both positive and negative, depending upon context (Isaac-Renton et al. 2014; Schmid et al. 2014). Introduced from western North America, provenance trials began in the 1910s with coastal sources from southern Washington or northern Oregon exhibiting the best growth (Isaac-Renton et al. 2014 and citations therein). Nevertheless, interior sources exhibited the best adaptation to drought (Pharis and Ferrell 1966) and low temperatures (Rehfeldt 1977).

The analysis of Douglas-fir provenance trials by Isaac-Renton et al. (2014) illustrates the trade-off between capacity adaptation (growth potential and competitive ability) and survival adaptation. While provenance trials provide ample evidence of growth potential, the ability to survive extreme weather events is only apparent if an event challenges a provenance at a vulnerable growth stage. For example, seedlings are usually more susceptible to near-ground late spring frost or drought than taller or just larger trees with more extensive root systems. Thus, data from provenance trials should be augmented with physiological tests before recommending material transfers (Isaac-Renton et al. 2014).

As Douglas-fir has become practically naturalized in portions of Europe, reforestation of plantations is not immune to the effects of changing climate. Isaac-Renton et al. (2014) examined performance of provenances under two climate periods, a stable 1961–1990 baseline and a 30-year warming trend (1995–2009). They argued that the climate envelope of more southerly populations adapted to drier conditions has shifted northwards and new plantings should recognize this change.

Transformational adaptation under climate change

Transformational adaptation differs from other strategies in the tolerance of novelty and the introduction of climate-adapted material is a key feature. Current regulation and guidance on transferring plant material stresses the importance of locally adapted material of species within their historic ranges (Gustafson et al. 2005; McKenney et al. 2007; Bower et al. 2014). Under a changing climate, with the potential for greatly different conditions than exist today (e.g. Williams and Jackson 2007; Williams et al. 2007), local sources may no longer be adapted (Frank et al. 2017). Species will respond to climate change by adapting, migrating, or dying out (Aitken et al. 2008; Berg et al. 2010) and species have adapted to changing climate in the past (Jump and Penuelas 2005; Valladares et al. 2014; Boshier et al. 2015; Espeland et al. 2016). The prospect of rapidly changing climate and frequent extreme events, along with fragmentation of many landscapes, may overpower the ability of species to adapt (Chapman et al. 2014; Park et al. 2014; Pacifici et al. 2015) or migrate (Iverson et al. 2004; Pearson 2006; Corlett and Westcott 2013; Stanisci et al. 2016).

Assisted species migration (Williams and Dumroese 2013), where species or genetic material is moved or obtained from far outside current ranges, can overcome limitations on species movement but this challenges notions of native species (Davis et al. 2011) that are prevalent (Warren 2007; Fleishman et al. 2011; Shackelford et al. 2013; Dunwiddie and Rogers 2016; Mattioli et al. 2016). Specific issues that have been raised focus on the effect of the introduced material on the receiving ecosystem, such as invasiveness, hybridization, pests, or pathogens (e.g. Laikre et al. 2010; Byrne et al. 2011; Felton et al. 2013). In truth, a certain amount of invasiveness and hybridization may be desirable in assisted migration to facilitate establishment of new species or transfer of adaptive traits into native populations (Dumroese et al. 2015). The timing of when to move material is perhaps a more difficult question than what to move or where to move it (McDonald-Madden et al. 2011; Rout et al. 2013; Stanturf 2015). Moving material with high genetic variation is preferable, although may not be feasible for some species threatened by climate change (Aitken et al. 2008). Empirical evidence of adaptation, through provenance testing, will provide the strongest test of whether to operationally translocate species outside their native range (Breed et al. 2013; Rout et al. 2013) and to intentionally introduce novelty into ecosystems. Importantly, adaptation to changing climate will be an on-going process; even material adapted to future climate conditions must survive current climate environments when planted (e.g. Gray et al. 2011).

Three questions require thoughtful consideration and if possible, empirical investigation. First, how likely is the potential for successful movement of material? There are several methods available for examining how a species will respond to dispersing or being moved to a new location with a suitable future climate (e.g. Breed et al. 2013; Lunt et al. 2013; Rout et al. 2013) and all require some knowledge of species genetics and traits, which is often limited for non-commercial species. The second concern is the effect an introduced species may have on the receiving ecosystem (McLachlan et al. 2007; Mueller and Hellmann 2008; Laikre et al. 2010; Hewitt et al. 2011; Pedlar et al. 2011). Addressing these concerns will be difficult, especially if the receiving ecosystem is undergoing change.

The third concern is how will moving material affect the donating ecosystem, the population of the migrating species, or both (Vitt et al. 2010; Williams and Dumroese 2013; Benito-Garzón and Fernández-Manjarrés 2015)? This is particularly important for rare or endangered species, where removal of material may affect the survival of the donating population (McLachlan et al. 2007; Seddon 2010; Vitt et al. 2010; Loss et al. 2011; Seddon et al. 2014). Other concerns are with regard to ethical and political concerns, if material is obtained from another country (Carnus et al. 2006; Schüklenk and Kleinsmidt 2006; Jackiw et al. 2015).

Transforming ecosystems for improved climate adaptation

Global change, the combined effects of climate change, globalization, land use change and interactions, is likely to result in significant novelty in forest ecosystems within a single tree generation (80–150 years). Adapting to novel conditions, particularly climate, will require transformational strategies that explore and develop plant material adapted to novel conditions. Transformation could be achieved by intentionally creating novel ecosystems, using biotechnology to create transgenic species to replace extinct foundational or keystone species or genotypes better adapted to future climate (e.g. *Castenea dentata* (Marshall) Borkh.; Jacobs 2007; Jacobs et al. 2013) or synthetic biology to create designer organisms with heretofore unknown capabilities (Stanturf 2015). This new material (whether species, provenances, or clones) must be adapted to current and future conditions and could be analogous, non-native species or genetically altered versions of native species (with genes from closely related or unrelated organisms, respectively, termed cisgenic or transgenic). One source for more adaptive genetic material is refugial populations (Keppel and Wardell-Johnson 2012; Hannah et al. 2014).

Refugial populations

Species can survive adverse climatic conditions in refugia, areas with more favourable conditions (Keppel et al. 2012). Stable climate over time often gives rise to species-rich refugia that maintain endemic species (Dynesius and Jansson 2000). Pleistocene glacial oscillations in northern Europe markedly shaped the distribution and genetic makeup of species (Comes and Kadereit 1998). Pleistocene refugia today are characterized by high genetic diversity and refugial areas may be distinctly different genetically. Areas that have been recolonized from different refugial regions often have higher genetic diversity but may show lower differentiation (Comps et al. 2001; Widmer and Lexer 2001; Petit et al. 2003; Bouriaud et al. 2015). Glacial ice covered northern Europe and temperate species survived in Iberian, Italian, Balkan refugia (Bennett et al. 1991; Taberlet et al. 1998). The area south of the Caspian Sea is a biodiversity hotspot (Akhani et al. 2010; Farashi and Shariati 2017) and recently has been proposed as a glacial refugia for temperate forest trees (Leroy and Arpe 2007).

Experience from Denmark

Danish forestry has a long tradition of using non-native tree species. Following the retreat of the glaciers the natural forests of Denmark included rather fewer species compared to temperate forests in North America and Asia and most of the country was deforested (Bradshaw 2005; Madsen et al. 2005). The forest restoration history of Denmark includes several forest generations over the past 200 years. Similar processes took place in other parts of north-western European lowlands including heathland tracts of northern Germany (Mather et al. 1998; Bradshaw 2004). Because Denmark is all lowland (highest elevation 170 m above sea level), there are no mountainous regions where natural forests could be protected against clearance and changes in land use. Therefore, little natural forest survived and definitely no virgin forest (Johannsen et al. 2013).

Forest landscape restoration

In Jutland (western Denmark), deforestation and impacts of shifting agriculture, grazing and fire created a highly degraded landscape that was dominated by heathland in the western and northern parts of the peninsula. The introduction of non-native species – particularly conifers – was needed both because the native broadleaves could not establish on the degraded heathlands (Madsen et al. 2005) and because society and people were in great need of the wood resources for construction and energy (Figure 3). Additionally, overgrazing and fire often destroyed the heather to an extent that the sandy soil was exposed to the wind and could start forming dunes that eventually threatened to cover houses and whole villages. These sandy soils were characterized by total lack of forest micro-climate and very acidic soil types (podzols) and as such the conditions for restoring forests

Figure 3. Survival and growth of seedlings planted on degraded sites in western Denmark were low and only non-native conifers could survive the conditions. Here are some of the last remnants of the 1st generation mountain pine (*Pinus mugo* Turra) planted to restore forest conditions 150 years ago. Such examples may still be seen in the coastal dune areas along the Danish coast. (Credit: Palle Madsen).

were extremely poor. Needless to say that all seed sources had disappeared centuries ago – and relying on natural regeneration or succession was not an option. The non-native mountain pine (*Pinus mugo* Turra) was one of the few species that could survive and grow on the degraded sites in western Denmark that were restored (afforested) over 150 years ago (Figure 3).

Danish forestry today

Danish forestry continues to rely extensively on non-native species. A large number of non-native tree species were tested to identify those sufficiently tolerant and productive under local conditions. Except for Scots pine (*Pinus sylvestris* L.), all productive conifer species – including Norway spruce (*Picea abies* (L.) Karst.) – are non-native. Non-native species are integrated in the close-to-nature approach to forest management currently in vogue, as long as they are used where they are adapted to site and can contribute to the formation of healthy continuous cover forests that later are capable of supporting natural regeneration of the desired tree species. Typical desired species among the non-natives with these characteristics are European and Japanese larch (*Larix decidua* Mill. and *L. kaempferi* (Lamb.) Carr.), Douglas-fir and European silver fir (*Abies alba* Mill.).

Silver fir in particular provides another example of introducing novelty into the Danish landscape and the relationship between adaptability and genetic variation. Through long-term field trials that were established in Denmark in 1934–1935, it was shown in the 1980s that Calabrian silver fir from southern Italy had superior health and growth compared to a wide range of silver fir provenances from southern and central Europe, from areas geographically and climatically more similar to Denmark (Larsen 1986). The Calabrian provenances have substantially greater genetic diversity than the other provenances (Bergmann et al. 1990), leading to the hypothesis that the Calabrian silver fir provenances of the coastal mountains facing the Strait of Messina were not exposed to the extreme conditions of the periglacial climate and therefore escaped genetic bottlenecks caused by the reduction of population size due to the harsh climate that affected the populations that spread into the European continent (Larsen 1994). Nevertheless, the Calabrian silver fir provenances were blocked from migrating north because the lowlands immediately north of Calabria were unsuitable for silver fir; therefore it was silver fir from the more northern and more genetically narrowed refugial populations that immigrated into Europe after the last glaciation.

The Danish example shows that an initial reliance on use of non-native species later created opportunities to reintroduce native species as well as other non-native species with desired functions (Figure 4). The challenge for the future is how to adapt to climate change; one idea is to search for new genetic material to transform Danish forests. This search has turned towards the Caspian forests of Iran.

New genetic material from Caspian forests

The Caspian forests are probably the largest forest area of temperate deciduous forest containing European flora that had little or minimal exposure to the two factors, ice age pauperization and human exploitation, that drastically reduced the number of species in Europe as well as their genetic diversity. The refugial populations in these Caspian forests may contain genetic material with potential for European forests and their ability to adapt to future challenges of climate change and new diseases and pests. Science-based statements about adaptability to climate, diseases and pests require establishment of field trials, while genetic diversity and population genetic structure and processes can be measured by DNA analyses. A new project is underway to contribute to the understanding of the evolutionary processes that European forest tree species have undergone

Figure 4. Restored forest landscapes on formerly degraded land in Denmark; here are the highly productive mixed stands of Norway spruce (*Picea abies* (L.) Karst.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), a novel forest ecosystem with non-native tree species in Denmark. (Credit: Palle Madsen).

as a function of selection pressure (ice ages/human influence) and isolation (refugial conditions) and how these processes have influenced genetic diversity and adaptive potential of the tree species. Eventually, this material may be used to transform Danish forests to adapt to global change. We briefly describe this effort as an example of the kind of "risky" research (Park et al. 2014; Stanturf 2015) needed to prepare for a novel future.

Caspian forests

South of the Caspian Sea in Iran, the species rich Caspian forests cover the north facing slopes of the east-west tending Elburz Mountains. Rising up 3000–5000 m, these slopes receive heavy rainfall and are covered by 1.8 million hectares of Caspian forests, of which 100,000–200,000 hectares are considered pristine forest, as inaccessibility has limited utilization and human influence. The Caspian forests date back to before the Pleistocene (more than 2.6 million years ago), previous to the repeated advances and retreats of the glacial ice masses farther north in Europe. The distributions of forest species have shifted slightly during the changing climates of the glacial and interglacial periods (Sagheb-Talebi et al. 2014; Ravanbakhsh et al. 2016; and references therein) but they have persisted for millennia.

The Caspian forests have benefited from long-term continuity in forest cover (Ramezani et al. 2008) and today contain many tree species that are also indigenous in Denmark and Europe (Figure 5), for example *Ulmus glabra* Huds., *Carpinus betulus* L., *Fraxinus excelsior* L. and *Sorbus torminalis* (L.) Crantz (Sagheb-Talebi et al. 2014), as well as a number of endemics, including *Acer velutinum*, *Quercus castaneifolia* C.A.Mey and *Pyrus boissieriana* Buhse. Caspian forests also contain *Zelkova carpinifolia* (Pall.) Dippel, *Pterocarya fraxinifolia* (Lam.) Spach, *Parrotia persica* (DC.) C.A. Mey., *Gleditschia caspica* Desf. and *Populus caspica* (Bornm.) Bornm., Arcto-Tertiary relicts that became extinct in other regions (Akhani et al. 2010; Sagheb-Talebi et al. 2014). This is consistent with climate modelling that showed the climatic conditions in the region of the Caspian forests were suitable for temperate broad-leaved trees during glaciations (Leroy and Arpe 2007).

The Caspian forests' genetic pools are considered to be closely linked or related to the initial populations and genetic diversity. The forests have only to a lesser extent been affected by paleoclimate fluctuations compared to corresponding deciduous forests in Europe, North-east America and the Far East (Adams and Faure 1997). Especially in Europe, the flora faced geographical barriers to migration caused by the east-west mountain ranges and the Mediterranean Sea (Hewitt 1999), resulting in limited and unfavourable refugial areas to survive the glacial advances. As a result of these barriers, species were eliminated from the continent or their population sizes reduced to such a degree that genetic variability has been reduced considerably (Hewitt 2000).

A gene pool for the adaptation of European forests?

A new project will test whether species and provenances from the Caspian forests possess greater genetic diversity and superior resistance (physiological adaptability) and resilience (evolutionary adaptability) as compared to comparable Danish/European forest tree seed sources. The intent is to collect seed from 6 selected tree species in the Caspian forests, each represented by up to 9 provenances. The seed will be used to establish provenance trials in afforestation areas in Denmark and Iran. The trials will also include European/Danish reference provenances and a comparative study for Caspian and European species in Denmark and Iran. Test material will be subject to quantitative genetic analyses in additional fast-track single tree plot trials. The DNA of all 6 species will be analysed to compare genetic diversity between the Caspian and Danish/European forests, as well as to describe the population genetic structure of the source populations. The provenance trials will be a unique infrastructure for the next decades for studies of forest

Figure 5. A chestnut-leaved oak (*Quercus castaneifolia* C.A.Mey) more than 600 years old in the Caspian forest of Iran. This tree is 45 m tall with a diameter at breast height of more than 2 m. (Credit: Palle Madsen).

tree adaptability and climate change that complements existing provenance trials in Denmark (Kjær et al. 2014; Myking et al. 2016) and the experience in Iran with 33 conifer species and provenances trials along longitudinal and latitudinal transects in the Caspian region. Promising species from these 25 year-long trials are *Pinus nigra* Arnold, *P. sylvestris* L., Douglas-fir, *Abies nordmanniana* (Steven) Spach), *P. abies* (L.) Karst. and *Sequoia sempervirens* (D. Don) Endl.

Assisted migration: a final comment

Foresters have much experience with moving woody species to new environments and should be able to identify likely successes and avoid potential adverse effects. Refugial populations may provide material, whether analogous species or genetic material for breeding programs. Empirical investigations, such as the provenance trials underway in Denmark and Iran, will provide short-term answers and a valuable resource for long-term investigations. The need for restoration, already significant, will only increase due to extreme climatic events, altered climate means and land use change. Although much uncertainty surrounds decisions of when to introduce novelty into ecosystems, the most critical ecosystems are those where climate and land use are projected to change rapidly (Stanturf 2015). Extreme events will provide opportunities for changing species or genetic composition of forests to reduce vulnerability to future climate alterations; preparing for transformational adaptation requires risky research today to prepare for events in the future (Sarr and Puettmann 2008; Park et al. 2014).

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