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Reproductive modification in forest plantations: impacts on biodiversity and society

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Summary

Genetic engineering (GE) can be used to improve forest plantation productivity and tolerance of biotic and abiotic stresses. However, gene flow from GE forest plantations is a large source of ecological, social and legal controversy. The use of genetic technologies to mitigate or prevent gene flow has been discussed widely and should be technically feasible in a variety of plantation taxa. However, potential ecological effects of such modifications, and their social acceptability, are not well understood. Focusing on *Eucalyptus*, *Pinus*, *Populus* and *Pseudotsuga* – genera that represent diverse modes of pollination and seed dispersal – we conducted in-depth reviews of ecological processes associated with reproductive tissues. We also explored potential impacts of various forms of reproductive modification at stand and landscape levels, and means for mitigating impacts. We found little research on potential reactions by the public and other stakeholders to reproductive modification in forest plantations. However, there is considerable research on related areas that suggest key dimensions of concern and support. We provide detailed suggestions for research to understand the biological and social dimensions of containment technologies, and consider the role of regulatory and market restrictions that obstruct necessary ecological and genetic research.

I. Introduction

The Earth's forests and associated biodiversity supply vast quantities of ecosystem services and products, including clean water, human and wildlife habitat, erosion control, carbon storage, medicines, and wood, chemical and energy products. Increases in the global human population (projected to grow from 7.1 to 8.3 billion by 2030) are expected to dramatically increase demand for forest products, such as timber by 129 million m^3 (FAO *et al.*, 2012). Resource extraction has traditionally come at the cost of forest loss and degradation, with a loss of *c.* 13 000 ha yr^{-1} (FAO *et al.*, 2012), which, in turn, drives biodiversity loss (Pimm *et al.*, 2014) and declines in ecosystem services (Gamfeldt *et al.*, 2013). Tree plantations are recognized as a partial solution (Brockerhoff *et al.*, 2008), as they usually have higher rates of wood volume accumulation than natural forests. Approximately 35% of the world's wood supply is generated by plantations, yet they comprise only 5% of the global forest area (FAO, 2010).

Tree breeding, increasingly accompanied by genomic methods, is ubiquitous in plantation management and is a major contributor to high rates of plantation productivity. In recent years genetic engineering (GE) – defined here as the direct and asexual alteration of DNA in living organisms – has been proposed as a new tool for tree breeding. Because GE can be used for changing native genes or transferring in novel functions, it has the potential to produce a variety of modified or novel traits. A large body of field research has shown that GE methods appear capable of delivering improvements to plantation productivity, wood processing, pest resistance or chemical products (FAO, 2010; Häggman *et al.*, 2013; Table 1). In some cases, the improvements can be substantial, such as elevating productivity in the field by *c.* 20% in poplar (Klocko *et al.*, 2014; Lu *et al.*, 2014; Ault *et al.*, 2016). However, the movement of seeds and pollen from GE plantations to feral and wild populations (hereafter termed 'gene flow') has been highly contentious in its regulatory treatment, public acceptance and possible impacts on markets. For example, pollen 'contamination' of non-GE products, an important economic problem with GE crops, may be even more difficult with GE plantation trees as a result of their typically longer dispersal distances. Pollen from GE eucalypts (that might contaminate honey products) was cited as a concern related to the growing commercial use of GE eucalypts in Brazil (Petermann, 2015) – where GE reproductive modification is illegal – and was a contributing factor to vandalism of company glasshouses (Marty, 2015).

Table 1 Examples of field trials of genetically engineered (GE) trees that have showed efficacy or promise in delivery of target traits

Tree species	Trait	Reference
American Chestnut *Castanea dentata*	Fungal blight resistance	Maynard *et al.* (2009); Zhang *et al.* (2013)
American Elm *Ulmus americana*	Dutch elm disease resistance	Newhouse *et al.* (2007); Sherif *et al.* (2016)
Silver Birch *Betula pendula*	Fungal rust resistance	Pasonen *et al.* (2004)
Poplar		
Populus tremula × alba	Biomass allocation	Lu *et al.* (2015)
P. tremula × alba	Tree size	Elias *et al.* (2012)
P. tremula × alba	Improved pulpabillity	Pilate *et al.* (2002); Coleman *et al.* (2012); Mansfield *et al.* (2012)
P. tremula × alba	Decreased lignin	Franke *et al.* (2000); Pilate *et al.* (2002)
P. tremula × alba	Specialty chemical production	Costa *et al.* (2013)
P. × canescens	Reduced isoprene emissions	Behnke *et al.* (2012)
P. tremula × alba	Nitrogen assimilation	Jing *et al.* (2004)
P. trichocarpa × deltoides, *P. tremula × alba*, *P. tremula × tremuloides*, *P. trichocarpa × nigra*	Herbicide tolerance	Meilan *et al.* (2002); Ault *et al.* (2016)
P. nigra, *P. deltoides × nigra*, *P. trichocarpa × deltoides*	Insect resistance	Hu *et al.* (2001); Klocko *et al.* (2014)
P. davidiana × bolleana	Salt tolerance	Yang *et al.* (2015)
P. alba	Flowering control	Klocko *et al.* (2016b)

In order to mitigate the social and biological problems of gene flow, GE methods that would reduce or prevent gene flow have been developed, but their potential impacts on biodiversity and society have received limited attention. Removal of pollen and/or seeds could obviously impact pollinators, as well as nectar- and seed-consuming organisms, and thus deserves careful consideration for each potential application so that this potential fix to the problem of gene flow is used judiciously and does not needlessly reduce the benefits of GE traits, or exacerbate rather than attenuate global impacts of plantations on biological diversity.

The primary goals of this paper are to evaluate the potential ecological impacts that modifications to forest tree reproduction might have on biodiversity, contextualize these impacts by comparing them to effects of other forms of forest management on reproductive activity, and examine how reproductive modification technology is expected to affect public, interest group and government responses. We focus primarily on the potential biodiversity and social impacts of GE reproductive modification; the impacts of other types of GE plantation modifications and the potential consequences of gene flow from GE plantations (when allowed or encouraged) have been discussed elsewhere, including in a recent compendium volume on GE forest biotechnologies (Vettori *et al.*, 2016).

II. Impacts of reproductive modification

We begin by outlining methods for GE of reproduction in forest trees. Then, to help interpret the significance of GE modifications to reproduction, we discuss the extent that forest management itself impacts tree reproduction. Next, we discuss the extent that various organisms utilize reproductive resources in our target genera. We conclude by considering the social factors that could influence acceptance or rejection of GE reproductive modification. Our methods for literature searches related to biodiversity and social dimensions are provided in Supporting Information Notes S1. These searches were structured to gather information related to a number of explicit hypotheses (Notes S2).

1. GE reproductive modification

There are a variety of potential and demonstrated options for GE-based reproduction modification in trees (reviews in Brunner *et al.*, 2007; Vining *et al.*, 2012). In addition to the goal of containment, reproductive modification also has been sought as a means to improve vegetative growth by increased allocation of photosynthetic resources (Strauss *et al.*, 1995), reduce the production of allergenic pollen and decrease nuisance reproductive tissues in urban trees. Most published studies of GE have focused on male-sterility because pollen is the main source of long-distance spread and seed propagation would allow for continued sexual breeding. One method for obtaining male-sterility, genetic ablation (i.e. cell elimination), was first developed and commercialized in agriculture, and is effective and reliable in field trials of *Populus*, *Eucalyptus* and *Pinus* (Zhang *et al.*, 2012; Elorriaga *et al.*, 2014; Fig. 1). However, because many intensively grown forest trees, most notably poplars and eucalypts, have seeds that can travel large distances by wind, water or animals, research also has focused on achieving complete bisexual (male and female) sterility. Both poplar and eucalypt plantations are widely established via vegetative cuttings, such that loss of seed production will still allow for tree propagation and establishment using current methods. Published results for achieving female or bisexual sterility have emphasized suppression of key flowering genes by RNA interference (Klocko *et al.*, 2016b; Fig. 2), a method that can be highly stable in field-grown trees (Li *et al.*, 2008). Direct editing of floral genes by use of CRISPR-Cas nucleases or similar approaches should be even more stable as entire genes can be deleted (Elorriaga *et al.*, 2015), but to our knowledge, gene-edited trees have yet to be tested in the field. Other methods that have been proposed for trees, but not yet demonstrated in the field, include the use of developmentally inducible recombinases to excise (i.e. to selectively remove from the genome) GE-modified genes during the formation of gametes. This approach would allow normal flowering yet little or no release of transgenes. Genes that suppress the age-related onset of reproduction also are potential targets for breeding or GE, as a wide array of floral suppressor genes has been identified in basic plant research (Pajoro *et al.*, 2014).

A common concern is that containment will be incomplete or unstable, or that asexual forms of dispersal will still allow for gene flow (Brunner *et al.*, 2007). In poplar, which has been widely studied, field research and simulations show that even incomplete or unstable male and female sterility would still provide high levels of genetic containment in various scenarios, including when linked to a strong fitness-promoting gene such as one giving resistance to an important herbivore of poplar (DiFazio, 2002; DiFazio *et al.*, 2012). Vegetative spread was also found to be a weak means of dispersal compared to pollen and seed. It is possible to modify organisms to prevent or slow vegetative spread, such as by preventing rooting except in the case of gene induction. However, to our knowledge, such methods have never been shown to be effective and vegetative spread can often be readily controlled by forest management rather than genetic methods (e.g. by scouting for and removing root and branch sprouts within and near to plantations). It also appears feasible to engineer post-flowering forms of containment by targeting genes required for pollen tube growth or fertilization, or genes that take part in embryogenesis. Many such genes have been characterized in model plants (Wang *et al.*, 2008; De Smet *et al.*, 2010), which might enable the production of floral and fruit organs with essentially normal nutritive value for biodiversity, but without the possibility of propagule growth and development. However, to our knowledge, such methods – although widely discussed for crops and for which there are a number of patents for reversible forms – have not been developed or field-tested in crops or trees (Lombardo, 2014). Given the wide scope for continued genetic innovation as knowledge of genes, development and methods for genetic modification grow, we can expect to see many refinements and new forms of genetic containment technologies in the future.

2. Impacts of forest management on reproductive activity

Intensive forest management practices often strongly influence reproductive activity. Perhaps the most extreme examples are short rotation bioenergy plantations that are managed on a one- to few-year coppice system (Santangelo *et al.*, 2016). Trees such as poplars are densely planted and literally cut-off near ground level during annual or semi-annual harvests, allowed to re-sprout from the roots, and then cut and re-sprouted for multiple harvest cycles.

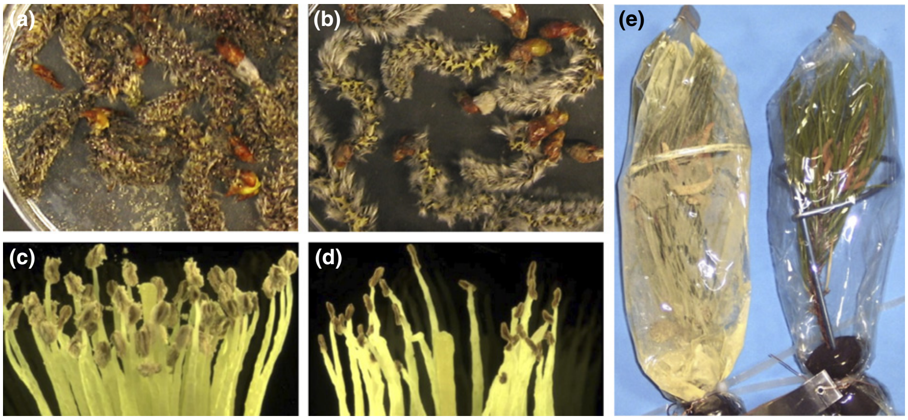

Fig. 1 Barnase expression leads to male sterility in field-grown trees. Male catkins of *Populus tremula* × *tremuloides* clone INRA 353-53 showing pollen release in Petri dishes from (a) control but not from (b) barnase trees (S. H. Strauss, unpublished; scientific background in Elorriaga *et al.*, 2014). *Eucalyptus occidentalis* flowers of (c) control and (d) barnase (note shriveled anthers that are not releasing pollen). (e) *Pinus rigida* × *taeda* male cone clusters of GUS control (left) and barnase (right) in pollen isolation bags. Control flowers shed large quantities of pollen grains, whereas pollen grains were absent from barnase flowers. Panels (c–e) reprinted with permission from Zhang *et al.* (2012).

Fig. 2 RNAi of floral genes is effective at altering tree floral morphology and fertility in field trials. (a) Wild-type (WT) female poplar catkins with well-developed carpels, (b) female sterile RNAi-LFY poplar catkin lacking externally visible carpels (Klocko *et al.*, 2016b), (c) female sterile RNAi-AG poplar catkin with replicated carpels (unpublished data, Strauss Lab), (d) WT female sweetgum flower with numerous white stigmas, (e) female sterile RNAi-AG sweetgum with stigmas converted to leaf-like projections (Klocko *et al.*, 2016c), (f) WT apple flowers with five petals, 20 stamens and five styles, (g) RNAi-AG apple flowers with anthers and styles converted to petals and reduced male and female fertility (Klocko *et al.*, 2016a).

Given this early harvest, trees are kept in a largely juvenile phase of fast growth with little or no flowering. However, even in longer rotation forest plantation systems, trees normally do not become reproductively active for several years, and the high planting density common to most systems (to suppress weeds, promote height growth and stimulate branch pruning), further delay the onset of reproduction and reduce the intensity of flowering and fruit production.

Thinning, or low natural stocking, has been associated with increased reproductive activity in a number of studies. For example, Verkaik & Espelta (2006) reported that Aleppo pine (*Pinus halepensis* Mill.) showed two- to six-fold increases in the number of new cones produced per tree in thinned stands compared to unthinned stands. Thinning also led to a four-fold increase in the percentage of newly reproducing trees. Benefits of thinning can last for 5 yr or more, as in *Pinus taeda* (Kozlowski *et al.*, 2012). This common trend (i.e. negative correlation between reproduction and stand density) was supported in 15 of 18 studies on conifer species (Table 2). Exceptions to this trend were observed in both wild stands (Moya-Laraño *et al.*, 2007; Ruano *et al.*, 2015) and seed orchards (Copes & Bordelon, 1994), perhaps because densities already were quite low, or as a result of other environmental factors known to affect flowering intensity (e.g. fertilization and irrigation in seed orchards).

Intensive genetic selection for rapid growth can further reduce the onset or intensity of reproduction, especially where propagation systems do not bias propagules toward those that flower early and most intensively (e.g. young seed orchards). In maritime pine (*Pinus pinaster*), Santos-del-Blanco *et al.* (2015) reported that a single cycle of selection for timber yield decreased the proportion of reproductive trees (51% in selected group vs 66% in control group), delayed the age and size at first reproduction, lowered the reproductive-to-vegetative allocation ratio, and affected the proportion of protandrous vs hermaphroditic individuals.

3. Stand-level biodiversity impacts

Modifying tree reproduction and changes in resources In order to interpret the potential impacts of flower modification on biodiversity, we need to be able to interpret how the impairment of plant reproduction can influence resources, which may then influence communities and ecosystem processes in a diversity of ways (Fig. 3). Impairing flower reproduction may alter the availability of pollen, nectar, fruits and seeds. Understanding both how tree reproductive resources are used by animals, and the nature and timing of changes in reproductive activity, are important for interpreting potential effects and may vary widely among taxa (Fig. 4). For example, alterations of male vs female flowering, changes in the time of year that flowering occurs and changes in the year of onset during a tree rotation will have differential impacts on dependent organisms. As discussed above, genetic methods can bring about different floral modifications, including a complete absence of flowers, pollen-less flowers, and (at least in theory) ecologically normal flowers, fruits and seeds whose pollen and seed are unable to give rise to viable progeny, or lack transgenes.

Table 2 Impact of stand density on flowering and seed production.

Species	Stand type	Measurement	Density	Density/reproduction association	Source
Aleppo pine (*Pinus halepensis* Mill.)	Wild	Cone production per tree	800–130 000 trees ha^{-1}	Negative	Alfaro-Sánchez *et al.* (2015)
Aleppo pine (*Pinus halepensis* Mill.)	Wild	Cone production, seed production	n/a	Negative	Reviewed by Ayari & Khouja (2014), which discussed studies done by Goubitz *et al.* (2004), Espelta & Verkaik (2007), Moya *et al.* (2008, 2009) and Ayari *et al.* (2012)
Aleppo pine (*Pinus halepensis* Mill.)	Wild	Cone production per ha	7089–61 145 trees ha^{-1}	Positive	Moya-Laraño *et al.* (2007)
Aleppo pine (*Pinus halepensis* Mill.)	Wild	Cone production per ha	Thinned: 1000 trees ha^{-1}; Unthinned: 5000–9800 trees ha^{-1}	Negative	Verkaik & Espelta (2006)
Loblolly pine (*Pinus taeda*)	Wild	Cone production per tree, Seed production per tree	n/a	Negative	Reviewed by Barnett & Haugen (1995), which discussed studies done by Wenger (1954) and Grano (1970)
Loblolly pine (*Pinus taeda*)	Wild	Flower bud production per tree, cone production per tree	n/a	Negative	Kozlowski *et al.* (2012)
Loblolly pine (*Pinus taeda*)	Plantation	Cone production per tree, number of seeds per cone, seed viability	Average stocking ranged from 50 to 770	Negative (cone production per tree vs stand density); None (number of seeds per cone and seed viability vs stand density)	Florence & McWilliam (1954)
Slash pine (*Pinus elliottii*)	Wild	Cone production per tree seed production per tree	n/a	Negative	Reviewed by Barnett & Haugen (1995), which discussed studies done by Cooper & Perry (1956), and Halls & Hawley (1954)
Slash Pine (*Pinus elliottii*)	Plantation	Cone production per tree, cone production per acre, number of seeds per cone, seed viability	Average stocking ranged from 60 to 320	Negative (cone production per tree vs stand density); Positive/negative (cone production per acre vs stand density; increased with closer spacing when stocking < 100–120 trees per acre, then decreased when tree spacing became smaller); None (number of seeds per cone and seed viability vs stand density)	Florence & McWilliam (1954)

Table 2 (Continued)

Species	Stand type	Measurement	Density	Density/reproduction association	Source
Shortleaf pine (*Pinus echinata* Mill.)	Wild	Percentage of sound seeds per tree	Released: basal area 14 m^2 ha^{-1}; Unreleased: basal area 28 m^2 ha^{-1}	Negative	Grayson *et al.* (2002)
Shortleaf pine (*Pinus echinata* Mill.)	Wild	Cone production per tree, seed production per tree	n/a	Negative	Reviewed by Barnett & Haugen (1995), which discussed studies done by Phares & Rogers (1962) and Grano (1970)
Longleaf pine (*Pinus palustris*)	Wild	Cone production per tree	n/a	Negative	Reviewed by Barnett & Haugen (1995), which discussed studies done by Allen (1953) and Croker (1952)
Maritime pine (*Pinus pinaster* Aiton)	Wild	Seed density, increase in seed density	45–188 trees ha^{-1}	Positive (seed density vs stand density); Negative (increase in seed density vs stand density)	Ruano *et al.* (2015)
Red pine (*Pinus resinosa*)	Wild	Cone production per tree	n/a	Negative	Wisconsin Department of Natural Resources (2010)
Western white pine (*Pinus monticola*)	Seed production area	Strobilus production per tree, seed production per tree, sound seed per cone	n/a	Negative (strobilus and seed production per tree vs stand density); None (number of sound seeds per cone vs stand density)	Barnes (1969)
Hoop pine (*Araucaria cunninghamii*)	Plantation	Cone production per tree, number of seeds per cone	Average stocking ranged from 100 to 600	Negative	Florence & McWilliam (1954)
Spanish fir (*Abies pinsapo*)	Wild	Cone production per tree, number of seeds per cone, seed viability	n/a	Negative (cone production vs stand density); Positive (number of seeds per cone and seed viability vs stand density)	Arista & Talavera (1995)
Douglas fir (*Pseudotsuga menziesii*)	Seed orchard	Cone production per tree, seed production per tree	Tree spacing 12 ft vs 24 ft within rows spaced 24 ft apart	None	Copes & Bordelon (1994)

n/a, not available.

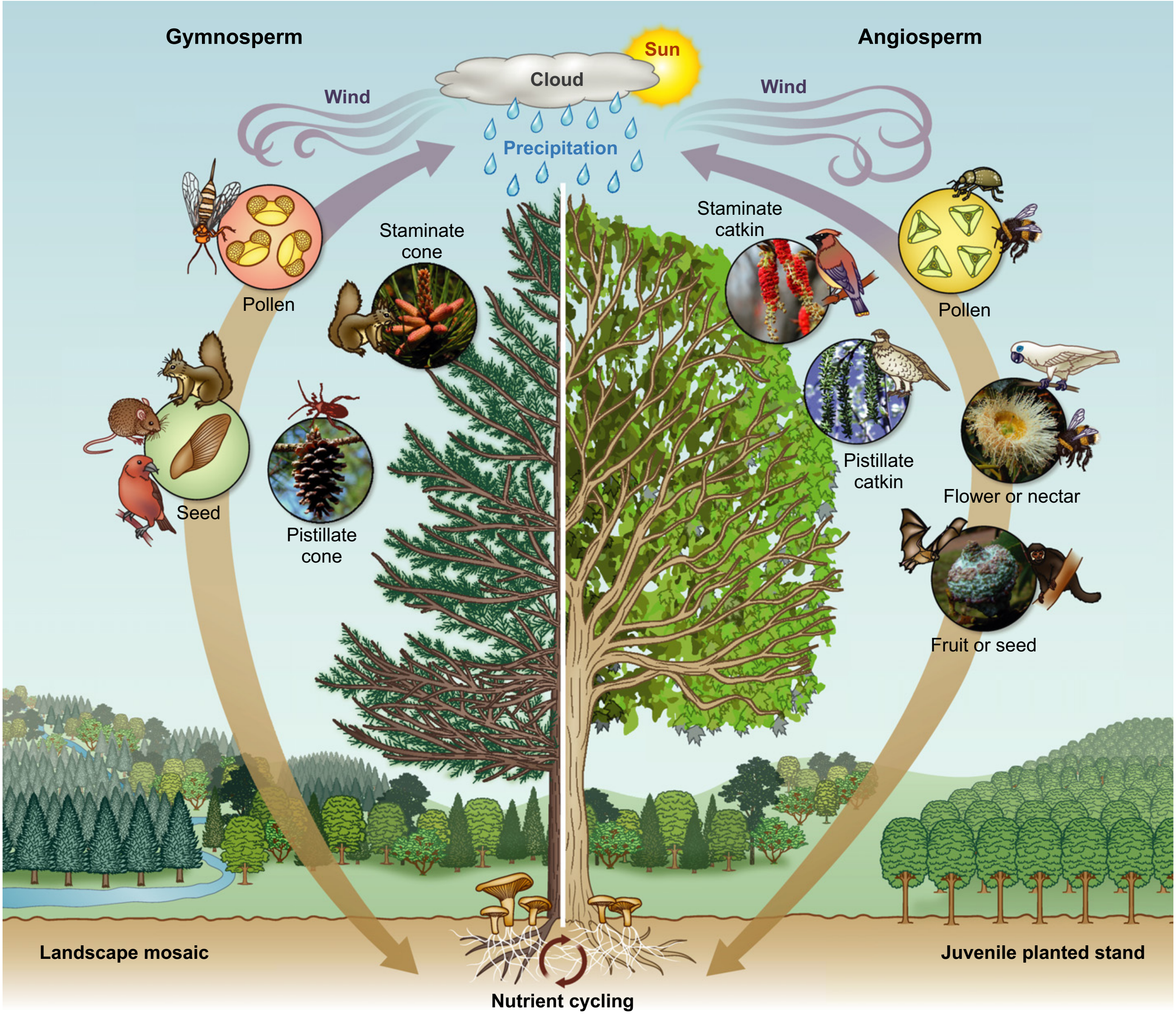

Fig. 3 Schematic overview of potential tree reproduction–biodiversity relationships in our focal gymnosperm (*Pinus*, *Pseudotsuga*) and angiosperm (*Populus*, *Eucalyptus*) genera. Circles with nearby organisms show the diversity of reproductive structures, which species may use or consume. Arrows show how reproductive structure deposition to soil or water, or contributions to local air masses, may affect nutrient cycling or local climate. The stands near the bottom show how reproductively modified trees are expected to be a part of juvenile, often mono-species plantations, and parts of landscape mosaics of wild stands and plantations of diverse ages and species compositions.

The relative impacts of floral modification by GE will depend on the plantation system in place and on natural environmental variation. Even without GE floral modification, resources from flowering can be extremely rare, either due to short-rotation harvests occurring largely before reproductive onset (e.g. bioenergy plantations; Munsell & Fox, 2010) or when flowering occurs late in a rotation or at a low level due to high stand density, as discussed above. In these situations, resources from reproduction are limited or absent in existing plantations, such that flower modification may have negligible consequences for altered resource distribution. In many plantations, resources from reproduction such as pollen, nectar and short-lived seeds may only be available during brief times of year, such that those resources are only available to certain members of the community and for a restricted period of time (Table 3). Across plantation tree species, the type of reproductive output, its quantity (e.g. seedfall or biomass of pollen) and its nutritive value, will vary. Natural environmental variation can also exert strong effects on reproductive resources, both due to variation in weather (e.g. moisture stress; Yuccer *et al.*, 2003) and climatic cycles. Many tree species fail to reproduce for many years then flower heavily in others (masting), with flowering associated with complex climate and weather variation (e.g. Sakai *et al.*, 2006). Many conifers, including our focal genera *Pinus* and *Pseudotsuga*, have well-known masting cycles (Koenig & Knops, 1998). In

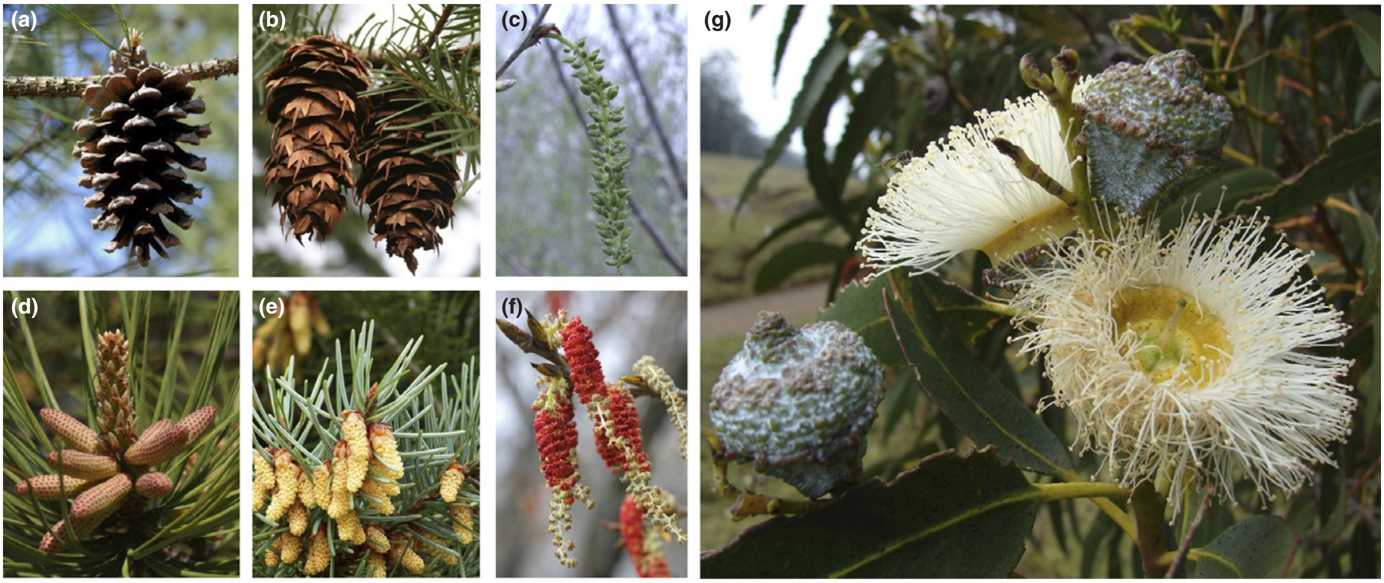

Fig. 4 Reproductive structures of *Pinus*, *Populus*, *Pseudotsuga* and *Eucalyptus*. Pistilate cones and catkins of (a) *Pinus taeda*, (b) *Pseudotsuga menziesii* and (c) *Populus alba*. Staminate cones of (d) *P. taeda*, (e) *P. menziesii* and staminate catkins of (f) *P. deltoides*. (g) *Eucalyptus globulus* produces fruit and perfect flowers. Photograph in (c) by author Amy Klocko. Source for other images: http://bobklips.com/treeflowersmenu.html.

addition to this temporal variability, monoculture plantations also represent a spatial aggregation of floral resources. In agricultural contexts, monocultures of mass-flowering crops can impact pollinators both positively and negatively (Westphal *et al.*, 2006), implying that floral modification in mass-flowering tree plantations may also have impacts on pollinator populations, pollination services and honey production.

Resource consumers and biodiversity changes Although searches including terms for GE reproductive modification yielded > 400 results, we found no empirical studies of impacts of GE reproductive modification on biodiversity, thus all of the inferences below are based on studies of reproduction–biodiversity relationships in conventional plantations or wild stands.

Classifying animals into functional groups, rather than considering them taxonomically, facilitates understanding of the potential effects of resources changes on biodiversity. We analyze functional groups in terms of the morphological component(s) of the plant reproductive tissues that are fed upon. We begin with nectar (nectarivory) and pollen (palynivory) feeders, which we functionally lumped together with pollinators because they typically consume nectar and/or pollen rewards. We then consider florivory, which we define as consumption of whole or partial flowers before seed coat formation (McCall & Irwin, 2006). When pollination is successful, a range of organisms feed on seed (spermivory) and fruit (frugivory), both pre- and post-dispersal. These categories are helpful in understanding the animal taxa involved, but species often feed on multiple stages of plant reproductive tissues. In discussing the taxa potentially impacted, we highlight economically and culturally important species, as well as those that are legally protected. Organism–tree genus associations from the literature are summarized in functional groups in Table 4.

Nectarivory and palynivory Many consumers of nectar and pollen also are pollinators, typically defined as animal pollen vectors (i.e. they move pollen between different flowers). Pollinators represent a substantial component of animals that feed on plant reproductive tissues, however, not all nectarivores and palynivores are pollinators. There are cases where flower visitors consume pollen and/or nectar without transferring pollen between flowers. One example of this is nectar robbery where a flower visitor circumvents flower opening to remove nectar without contacting anthers or stigmas (Irwin *et al.*, 2010). Pollination as an interaction likely evolved from palynivory by beetles (Labandeira & Eble, 2000) although palynivory without at least some incidental pollen transfer may be rare given that most palynivores will visit multiple flowers and likely carry some pollen on their bodies. The exception is in monoecious or dioecious plants where palynivores may be able to focus exclusively on male flowers or plants. Three of our focal genera – *Pinus*, *Populus* and *Pseudotsuga* – are wind-pollinated and thus do not produce floral nectar (Fig. 4; Table 3). These taxa likely have a community of palynivores, although we could find no studies characterizing the pollen-feeding assemblages of these taxa.

The primary tree genus that is animal-pollinated and also the focus of transgenic developments is *Eucalyptus*, which has a diverse and substantial community of flower visitors that vary depending on geographic location and species. This list includes marsupials, birds and a diverse assemblage of insects (Table 4). In plantations without active pollination management, seed production is often low and pollen-limited (reviewed in Moncur *et al.*, 1995), which may result in reduced seed consumer abundance and/or richness compared with other land uses. Most *Eucalyptus* species provide copious and sugar-rich nectar resources (Moncur *et al.*, 1995), and beekeepers in many parts of the world will bring honey bee colonies to plantations during flowering to promote honey production

Table 3 Key reproductive characteristics and phenology of *Eucalyptus*, *Pinus*, *Populus* and *Pseudotsuga* that influence resources for animals

Tree genera	Species	Pollination	Seed dispersal	Age of first reproduction (yr)	Flowering period	Seed dispersal period	Years between seed production	Serotiny	Vegetative reproduction	Flowers	Nectar	Fruit	Seed weight (g)
Eucalyptus	*globulus*	Zoophilous	Anemochory	3–4	Year-round	Year-round	Year-round	None	Present	Present	Present	Capsule	0.002
	grandis	Zoophilous	Anemochory	2–3	April–May in Australia, August–November in USA	January–April	1	Present	Present	Present	Present	Capsule	0.002
	regnans	Zoophilous	Anemochory	20	January–May	January–April	1	Present	Present, weak	Present	Present	Capsule	0.006–0.013
Pinus	*taeda*	Anemophilous	Ambochory	5–10	Feb–April	Oct–Dec	3–13	Present	None	None	Rare/none	Capsule	0.025
	radiata	Anemophilous	Ambochory	5–10	Jan–Feb	Midwinter	.	Present	None	None	None	Cone	0.025
	sylvestris	Anemophilous	Ambochory	5–15	May–June	Dec–March	4–6	Present	None	None	None	Cone	0.006
	elliottii	Anemophilous	Ambochory	7–12	Jan–April	Sept–Nov	1–3	Present	None	None	None	Cone	0.029–0.033
Populus	*tremuloides*	Anemophilous	Anemochory	2–3	March–June	March–June	1	None	Present	None	Extrafloral	Catkin	0.0001–0.0002
	deltoides	Anemophilous	Anemochory	5–10	Feb–April	May–July	2	None	Present, uncommon	None	Extrafloral	Catkin	0.001
	trichocarpa	Anemophilous	Anemochory	10	March–June	May–July	3	None	Present	None	Extrafloral	Catkin	0.0002
Pseudotsuga	*menziesii*	Anemophilous	Anemochory	12–15	March–May	October–May	7	None	None	None	None	Cone	0.011–0.014

Sources of data: Krugman & Jenkinson (1974); Shepherd (1986); Bonner & Karrfalt (2008); Guries *et al.* (2010); http://Florabank.org.au; http://Worldagroforestry.org.

Table 4 Count of organisms associated with reproductive structures/products of *Eucalyptus*, *Pinus*, *Populus*, *Pseudotsuga*

Taxonomic group	Organism association	*Eucalyptus*	*Pinus*	*Populus*	*Pseudotsuga*	References
Birds	Catkin feeder	.	.	1	.	Jakubas *et al.* (1993), Lindroth & St Clair (2013)
	Florivore	4	.	1	.	Marsden & Pilgrim (2003); Guglielmo & Karasov (1995)
	Frugivore, Nectivore	3		.	.	Hingston & Potts (2005)
	Frugivore, Nectivore, Spermivore	1	.	.	.	Hingston & Potts (2005)
	Frugivore, Nectivore, Spermivore, Florivore	2	.		.	Hingston & Potts (2005)
	Nectivore	27		.	.	Leveau & Leveau (2011), Hingston *et al.* (2004a), Hingston & Potts (2005), Cecere *et al.* (2011), Calviño-Cancela & Neumann (2015), Bennett *et al.* (2014)
	Nectivore, Palynivore	2	.	.	.	MacNally & Horrocks (2000), Hingston *et al.* (2004a)
	Palynivore	7	.	1	.	Roulston & Cane (2000); Witmer (2001)
	Spermivore	1	13	.	6	Hingston & Potts (2005); Snyder *et al.* (1994), Summers & Proctor (1999), Summers (2011), Benkman & Parchman (2009), Williams (2009), Vander Wall (2008), Vander Wall (1994), Tomback & Achuff (2010), Thayer & Vander Wall (2005), Siepielski & Benkman (2007), (2004), Rumble & Anderson (1996), Parchman & Benkman (2008), Myczko *et al.* (2015), Mezquida & Benkman 2005, Johnson *et al.* (2003), Garcia-del-Rey *et al.* 2011), Christensen & Whitham (1993), Chen & Chen (2011), Benkman (2010), Benkman (1993), Barringer *et al.* (2012), Bardwell *et al.* (2001); Smith & Balda (1979)
Fungi	Palynivore	.	2	.	.	Hutchison & Barron (1997)
Invertebrates	Catkin feeder	.	.	1	.	Leatherman (2011)
	Hyphaevore	1	.	.	.	Mound (1998)
	Nectivore	77	.	.	.	Hingston *et al.* (2004a), Griffin *et al.* (2009), Menz *et al.* (2015)
	Nectivore, Palynivore	22	.	.	.	Hingston *et al.* (2004b), Simeão *et al.* (2015), Griffin *et al.* (2009), Oliveira-Abreu *et al.* (2014), Obregon & Nates-Parra (2014)
	Palynivore	5	9	.	.	More *et al.* (2010), Millar *et al.* (2003), Hilgert-Moreira *et al.* (2014), Arien *et al.* (2015), Araneda *et al.* (2015); Sivilov *et al.* (2011), Riley *et al.* (2011), Pernal & Currie (2000), Graham *et al.* (2006), Czechowski *et al.* (2008), Angelella & Riley (2010), Abdullah *et al.* (2014)
	Spermivore	.	11	.	12	Teste *et al.* (2011), Siepielski & Benkman (2004), Millar *et al*. (2003), Dormont & Roques (1999), de Groot & DeBarr (1998), Christensen & Whitham (1993), Bellocq & Smith (1994), Barringer *et al.* (2012); Mailleux *et al.* (2008), Smith & Balda (1979)
Mammals	Catkin feeder	.	.	1	.	Willson *et al.* (2012)
	Frugivore	.	1	.	.	Mikich & Liebsch (2014)
	Nectivore	1	.	.	.	McCartney *et al.* (2007)
	Nectivore, Palynivore	1	.	.	.	Dobson *et al.* (2005)
	Palynivore	1	.	.	.	van Tets & Hulbert (1999)
	Spermivore	.	35	.	9	Summers & Proctor (1999), Benkman & Parchman (2009), Vander Wall *et al.* (2008), (2003), (2002), (2000), (1995), (1994), (1993), Tomback & Achuff (2010), Thayer & Vander Wall (2005), Siepielski & Benkman (2004), Rong *et al.* (2013), Podruzny *et al.* 1999), Parchman & Benkman (2008), Molinari *et al.* (2006), Mezquida & Benkman (2005), Kuhn & Vander Wall (2007), Johnson *et al.* (2003), Hollander & Vander Wall (2004), Hamer & Pengelly (2015), Gunther *et al.* (2014), Elias *et al.* 2006), Costello *et al.* (2014), Christensen & Whitham (1993), Chen & Chen (2011), Brzeziński (1994), Briggs *et al.* (2009), Becker *et al.* (1998), Asaro *et al.* (2003); Smith & Balda (1979), Smith (1970), Trebra *et al.* (1998)
Microbiota	Palynivore	.	.	2	.	Masclaux *et al.* (2011)

Numbers represent a summation of records noting species and/or genera associated with reproductive structures/products. In some cases, multiple records came from the same reference. Reference order corresponds to organism count order in each row. References separated by commas indicate multiple references corresponding to one count. References corresponding to distinct combinations of feeding mode and tree species are separated by semicolons.

(Moncur *et al.*, 1995; Invernizzi *et al.*, 2011). However, honey bee colonies apparently cannot be sustained on *Eucalyptus* floral resources alone, likely due to the relatively low protein content of pollen (Moncur *et al.*, 1995; Invernizzi *et al.*, 2011). Among flower visitors are several species that are of conservation concern in some regions, including the Swift Parrot (*Lathamus discolor*) and the Blue-Eyed Cockatoo (*Cacatua ophthalmica*), which are endangered and vulnerable species that frequently feed on nectar, flowers and pollen (Marsden & Pilgrim, 2003; Hingston *et al.*, 2004b; Hingston & Potts, 2005). Two mammals, the Lesser Short-Tailed Bat (*Mystancina tuberculate*) and the Black Capuchin (*Sapajus nigritus*), also have been shown to consume *Eucalyptus* fruit and pollen (McCartney *et al.*, 2007; Mikich & Liebsch, 2014).

Florivory Although florivory includes consumption of, or damage to, pollen and ovules (or immature seeds) in addition to other floral structures (e.g. bracts, petals, pistils, stamens), here we exclude strict pollen/ovule consumption from florivory as already discussed. Florivory has been relatively understudied (McCall & Irwin, 2006) and there is little information on how florivory impacts the tree genera that are the focus of this review. One exception is the Douglas Squirrel (*Tamiasciurus douglasii*), which is known to consume entire mature pollen cones of Douglas-fir (*Pseudotsuga menziesii*; Maser *et al.*, 1981). Another exception is *Populus* catkins, as several bird species use them for food. Cedar Waxwings (*Bombycilla cedrorum*) consume male catkins of Eastern Cottonwood (*Populus deltoides*). In experimental feeding trials, Witmer (2001) showed that captive waxwings lost body mass on a diet of *Viburnum opulus* fruits unless their diet was supplemented by *P. deltoides* catkins, whose pollen was shown to be an important source of supplemental protein. Similarly, quaking aspen (*Populus tremuloides*) flower buds and catkins comprise a significant portion (66–100%) of the winter and spring diet of the ruffed grouse (*Bonasa umbellus*; Jakubas *et al.*, 1993), although its high amounts of secondary metabolites also reduce its nutritional value. Various bird species may also use *Populus* catkins indirectly as a source of invertebrate food. For example, long-snouted weevil (*Dorytomus* spp.) larvae feed on pollen grains within staminate catkins and may provide a supplemental food source for birds during energy-intensive migration (Leatherman, 2011).

Spermivory Seeds and plant ovules represent a rich resource utilized by various animals. We treat this separately from frugivory, or fruit consumption, which often also involves seed consumption, and which is covered below. Seed and ovule feeding (hereafter referred to as 'seed' for simplicity) can take place in various floral developmental stages and ecological contexts. Seeds can be consumed pre- or post-dispersal (Howe & Smallwood, 1982), by insect larvae that develop exclusively within a single seed and by vertebrates that consume many seeds over the course of a single day. In general, the mode of seed dispersal is of ecological importance for spermivory, given that wind- (or gravity-)dispersed seeds (including *Pseudotsuga*, *Populus* and *Eucalyptus*) tend to be of low nutritive value relative to most animal-dispersed seeds (including those of *Pinus*; e.g. Gautier-Hion *et al.*, 1985).

Two of our focal tree genera – *Populus* and *Eucalyptus* – are not considered animal dispersed and have relatively non-nutritious seeds that do not serve as a substantial resource for animal communities. For example, *Eucalyptus globulus* is considered gravity-dispersed and most seeds are estimated to fall within 20 m of the parent plant (Skolmen & Ledig, 1990). A study of this species in Spain, where it is an exotic, found no evidence of any seed predation or animal-mediated seed movement (Calviño-Cancela & Rubido-Bará, 2013). Similarly, *Populus* has small wind-dispersed fruits with single seeds that are unlikely to be an important food source for vertebrates (Zasada *et al.*, 1992).

However, the dichotomy between animal dispersal and wind/gravity dispersal is not perfect, and of one our focal genera, *Pseudotsuga*, is a counterexample. Its seeds are winged and thought to be dispersed primarily by wind and gravity (e.g. Fowells, 1965), but are food items for: a number of mammals including mice, voles, shrews and chipmunks (Gashwiler, 1970); birds including the Winter Wren (*Troglodytes hiemalis*), Pine Siskin (*Carduelis pinus*), Song Sparrow (*Melospiza melodia*), Golden-Crowned Sparrow (*Zonotrichia atricapilla*), White-Crowned Sparrow (*Zonotrichia leucophrys*), Dark-Eyed Junco (*Junco hyemalis*) and Purple Finch (*Haemorhous purpureus*) (Arno & Hammerly, 1977); and a range of insect seed predators (Strothmann & Roy, 1984). Relatively specialized feeders on *Pseudotsuga* seeds include the aforementioned Douglas Squirrel (Arno & Hammerly, 1977) and potential subspecies of red crossbill, including the Douglas-fir Red Crossbill (*Loxia curvirostra neogaea*; Parchman *et al.*, 2006).

Of our focal tree genera, spermivory is likely the most important in *Pinus*. Pine seeds are considered to be wind- or gravity-dispersed in *c.* 85 of the 110 species in the genus, with the remaining 25 or so considered to be primarily animal dispersed, including the well-known Clark's Nutracker (*Nucifraga columbiana*)–Whitebark Pine (*Pinus albicaulis*) symbiosis (Tomback & Linhart, 1990). A rich community of animals feed on pine seeds ('pine nuts' to human consumers), including from species that are considered wind-dispersed (e.g. Vander Wall, 2008). This includes several species of conservation concern including the Tenerife Blue Chaffinch (*Fringilla teydea*), a species endemic to Spain that primarily eats *Pinus sylvestris* seeds (Garcia-del-Rey *et al.*, 2011). Similarly, the Maroon-fronted Parrot (*Rhynchopsitta terrisi*) and Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*) are spermivores native to the southwest USA and Mexico that feed primarily on seeds from pines such as *Pinus ponderosa*, *P. menziesii*, *Pinus engelmanii* and *Pinus arizonica* (Snyder *et al.*, 1994).

Frugivory Frugivory, or consumption of fruit, technically only occurs in angiosperms because gymnosperms do not produce fruit (they are named for their naked ('gymno') seed ('sperm')). Thus, seed consumption in gymnosperms, including *Pinus* and *Pseudotsuga*, is considered spermivory. Of our target species, frugivory in the angiosperms – *Eucalyptus* and *Populus* – is not substantial, as discussed above under spermivory.

Specialization on resources The degree that species specialize on reproductive resources will influence the extent that altering reproduction will impact populations and communities. In general, it is frequently acknowledged that highly specialist pollinators (Waser *et al.*, 1996; Bascompte *et al.*, 2003) and frugivores (Ottewell *et al.*, 2014) are rare. This is particularly the case in temperate systems where interannual and seasonal variation in flower and fruit availability makes specialization an evolutionarily risky strategy (Waser *et al.*, 1996). For those species that do specialize on these resources, flower modification may have negative impacts. We expect that specialization will be less likely to occur when plantations use non-native tree species, but this will depend partially on evolutionary similarity between tree species and native species in the area, and the length of cultivation in the new geography. In addition, specialists may be uncommon in plantation forests (Bremer & Farley, 2010), such that flower modification may have few impacts because these species may already be absent.

4. Landscape-level impacts

Management practices often have effects beyond those observed at local scales; composition and configuration of habitats can have a considerable influence on biodiversity at regional and global scales (Turner, 1989; Haddad & Tewksbury, 2005). Such effects become particularly pronounced as landscapes become more homogeneous (i.e. beta-diversity is reduced; Van der Plas *et al.*, 2016). Given uncertainty about the degree that GE-induced changes to tree reproduction may influence habitat quality across taxa, here we consider five potential scenarios for landscape-scale effects: (1) creation of low-quality or nonhabitat, (2) plantations as permeable matrix, (3) the emergence of ecological traps, (4) changes in nutrient cycling; and (5) impacts on local and regional climate.

GE plantations as low-quality or nonhabitat Removal of reproductive structures is most likely to render habitats of reduced quality, or nonhabitat, for pollinators and seedeaters. Much has been written on the effects of habitat loss and fragmentation on native biodiversity over the past 20 yr. Ultimately, it is the spatial extent of habitat loss due to GE plantations across the landscape that will determine compatibility with biodiversity (Fahrig, 1998; Hanski, 1998). If GE plantations result in only minor habitat loss at the landscape scale (e.g. < 5–20%), we consider population-level effects to be highly unlikely (e.g. Andrén, 1994; Fahrig, 2003). At these levels of habitat loss, population declines should be marginal and remaining habitat would tend to be highly connected, which facilitates inter-patch dispersal. However, both theoretical (Fahrig, 1998) and empirical work (Andrén, 1994; Betts *et al.*, 2007) have indicated that thresholds exist where habitat decline results in disproportionate population declines. Mechanisms for such thresholds are many and include reduced dispersal capacity once landscapes become highly fragmented by nonhabitat (Hanski, 1998), Allee effects (i.e. positive density dependence; Fletcher, 2006; Schmidt *et al.*, 2015), and increased risks of predation and parasitism (Robinson *et al.*, 1995). The amount of GE plantation development that can take place at the landscape level before it compromises gamma diversity (i.e. the regional species pool: Ricklefs, 1987), ecosystem functioning and population viability of native species depends on the dispersal capacity of organisms to recolonize managed stands. In turn, this will be a function of the spatial configuration of plantations and the degree to which they impede animal movement (Root & Betts, 2016).

GE plantations as permeable matrix Although reproductively modified GE plantations may not serve as breeding habitat for pollen- and seed-dependent animals, for some species the cover provided by tree canopy may facilitate movement among patches (Brockerhoff *et al.*, 2008). In such cases, a matrix dominated by plantations could be preferable to other types of habitat loss that would occur through urbanization or agricultural development. We predict that mature forest-associated species are more likely to benefit from this positive 'matrix' effect. Conversely, for species that preferentially breed and disperse though early seral habitats (e.g. butterflies and many species of pollinators; Haddad & Tewksbury, 2005), closed-canopy GE plantations are more likely to constitute a barrier, thereby potentially reducing population viability.

GE plantations as ecological traps Organisms regularly depend on environmental cues to make habitat selection decisions. However, in anthropogenically altered environments, previously reliable cues may become maladaptive. In such cases, organisms can become 'trapped' by their behavioral responses, resulting in reduced survival or reproduction (Schlaepfer *et al.*, 2002). Given the novelty of GE reproductive modification, and the lack of studies about how organisms that feed on reproductive structures use them as cues, little is known about the degree that such plantations could constitute ecological traps. If native species select habitat based on structural cues associated with the forest rather than direct cues such as the pollen or seeds (as food), the potential exists for GE plantations to act as traps. In such cases, even small amounts of GE plantations could potentially have negative impacts on populations because individuals could be drawn from otherwise appropriate habitat toward suboptimal locations with reduced fitness. Simulated population models (Schumaker *et al.*, 2004) could assist in understanding the degree of 'trap' effect required in relation to other demographic parameters before substantial risks to populations are encountered. However, the biological knowledge on which such models must be built is presently lacking, in no small part due to the rarity of all types of GE plantations, reproduction-modified or otherwise (*c.* 0.00033% of plantation area: less than *c.* 500 ha, mostly poplars in China (Walter *et al.*, 2010; Häggman *et al.*, 2013; Vettori *et al.*, 2016)), in relation to a global plantation estate of *c.* 150–200 million ha (of total forest area of *c.* 4 billion ha; R. Sedjo, pers. comm., May 18, 2016).

Role of pollen in nutrient cycling Enriched with vegetation growth-limiting elements such as nitrogen, tree pollen may provide a significant supplement of macronutrients to forest ecosystems early in the growing season. For example, Perez-Moreno & Read (2001) found that a species of ectomychorrhizal fungus (*Paxillus involutus*) was able to consume nitrogen and phosphorus from the extensive pollen deposited by a member of our focal genera (*P. sylvestris*) and return a significant proportion of these nutrients to its host tree *Betula pendula*. They demonstrated experimentally that *Betula* individuals grown with pollen and mychorrizal symbionts contained significantly more nitrogen and phosphorus than those grown without pollen, resulting in increased seedling growth. However, compared to litterfall, overall nutrient inputs into forest ecosystems via pollen appear to be small. For example, Cho *et al.* (2003) found pollen deposition in temperate pine forests in Korea to be *c.* 0.3% that of total litterfall by weight, with nitrogen inputs corresponding to 1% and 6% of total nitrogen and phosphorus, respectively. Pine pollen may nonetheless be a significant source of nutrients during the critical early growing period. In single-species plantations of *Pinus* and other wind-pollinated species, however, such inputs would likely be the same or less than the loss of nutrients from pollen release.

Tree pollen may provide an important source of nutrients for freshwater ecosystems. Graham *et al.* (2006), for example, found that *Pinus* pollen enhanced productivity in a small (0.27 km^2) boreal lake system by increasing phosphorus and carbon availability. From May to June, an estimated 7 kg km^{-2} of pollen (0.5% P by weight) was deposited onto the lake, providing a potential subsidy of 10 kg of phosphorus. The increased levels of phosphorus (and correlated increases of carbon) were associated with significant increases in diatom, phytoplankton and zooplankton abundance around the time of pollen deposition.

Role of pollen in regional climates Changes in the abundance and types of tree pollen may significantly influence local and regional climate. Bioaerosols, including pollen grains present in large quantities, can alter cloud properties and influence atmospheric radiative forcing by scattering and absorbing solar and planetary radiation (Bonan, 2008; Després *et al.*, 2012). Pollen also has been shown to be an efficient source of cloud condensation nuclei (e.g. Pope, 2010; Steiner *et al.*, 2015), but its relative importance to cloud formation is unclear given that it is often at low density and of short duration compared to other natural and anthropogenic sources of such nuclei. As with most other reproductive modifications, the climatic impacts of modified pollen production would be highly scale- and context-dependent.

5. Social dimensions

Support and opposition for GE In addition to biological considerations, societal responses toward GE and related technologies can impact their adoption and regulation (e.g. Davison *et al.*, 1997; Frewer *et al.*, 2003, 2004; Costa-Font *et al.*, 2008; Gupta *et al.*, 2011; Lucht, 2015). Although specific studies on societal responses to reproductive modification in trees are scarce, research associated with more general use of GE in trees provides insight into whether people might reject or accept reproductive modification.

Concepts including attitudes, risk, knowledge and trust are related to acceptance of GE (Fig. 5). Attitudes involve evaluating an entity such as GE with some degree of favor or disfavor (Fishbein & Ajzen, 2010). Compared to agriculture, attitudes toward GE in trees and forests are less understood and there are only a few studies of attitudes about reproductive modification in forest trees (Strauss *et al.*, 2009). In a sample of students in multiple countries (mostly European), Kazana *et al.* (2015) found generally positive attitudes toward using GE of trees in plantations, but not in wild natural forests. In a sample of the public in the USA, Needham *et al.* (2015) found that attitudes were less favorable toward using GE in wild forests compared to other forestry techniques (e.g. breeding, planting, thinning), but GE was more favorable for addressing tree diseases (e.g. chestnut blight) compared to other forest impacts (e.g. climate change, increasing growth for timber; Fig. 6). GE also was more acceptable in native species compared to adding genes from exotics or distantly related species (Needham *et al.*, 2015). Attitudes toward GE also vary between experts (e.g. forest scientists, forestry agencies) and the public, with experts often having more favorable attitudes (Małyska *et al.*, 2014; Porth & El-Kassaby,

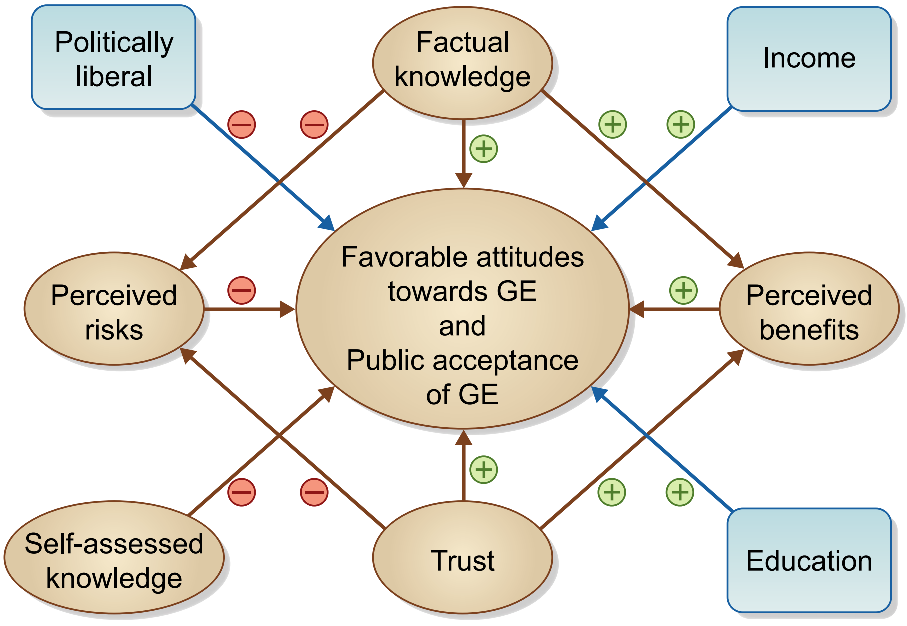

Fig. 5 Conceptual model of proposed relationships among favorable attitudes and public acceptance of genetic engineering (GE). +, positive relationship between concepts; –, negative association. Blue boxes, observed/directly measured single variables; brown ovals, latent concepts measured with multiple variables.

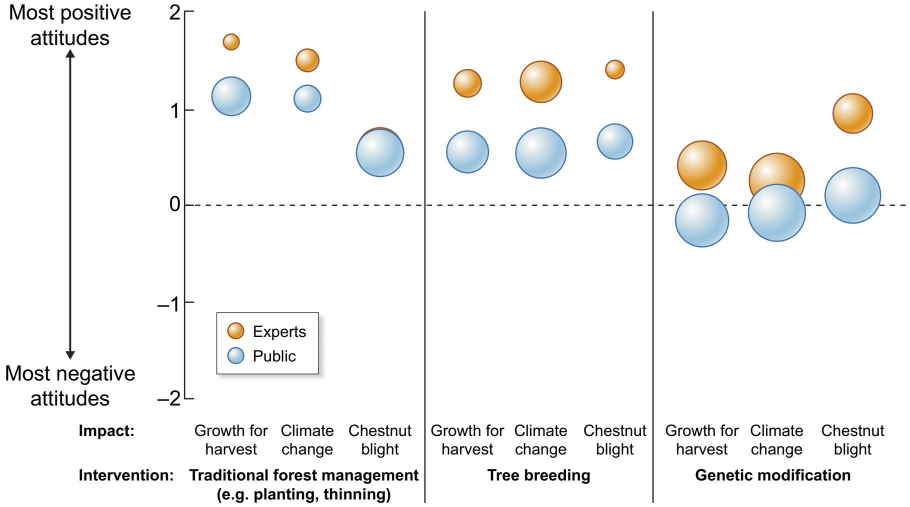

Fig. 6 Public and expert attitudes to forest health interventions in the USA. Survey results of public ($n = 278$) and expert ($n = 195$; scientists, agencies, companies and nongovernmental organizations involved in forest issues) attitudes toward using different interventions for addressing various forest health impacts (Needham *et al.*, 2015). Attitudes represent a composite index measured with four items on semantic differential scales (bad – good, foolish – wise, harmful – beneficial, disagree – agree; Cronbach's alpha reliability = 0.89–0.97). The middle of each bubble represents the index mean on the vertical scale. The size of the bubble represents the Potential for Conflict Index (PCI_2; Vaske *et al.*, 2010), where large bubbles ($PCI_2 = 1$) represent the least amount of consensus and greatest potential for conflict, and small bubbles ($PCI_2 = 0$) represent the greatest amount of consensus and least potential for conflict.

2014). Needham *et al.* (2015) found that, compared to the public, experts (scientists, agencies, companies and nongovernmental organizations involved in forest issues) had more positive attitudes toward GE in forestry (Fig. 6).

Risks and benefits of GE Most research on public responses to GE has focused on risk perceptions, which are subjective evaluations of threats posed by hazards (Slovic, 2000). In general, people express concern and skepticism toward new and unknown hazards that are not well-understood (Finucane & Holup, 2005; Rastogi Verma, 2013; Blancke *et al.*, 2015). Given its novelty, reproductive modification in trees is likely to be associated with risk factors such as newness, harm, dread, unnaturalness and unfamiliarity (Slovic, 2000; Sjöberg, 2004). Research examining public responses toward approaches for addressing forest impacts, for example, showed that biotechnologies (e.g. GE) were perceived as riskier than more well-known and familiar approaches such as planting and thinning (Needham *et al.*, 2015). Interestingly, cross-breeding with related species (e.g. American chestnut with non-native Asian chestnut) was considered riskier than transgenic approaches (i.e. inserting genes from unrelated species such as from bread wheat to the American chestnut), suggesting that perceptions of naturalness or familiarity may elicit different concerns because Asian chestnut species, although more closely related to the American chestnut than wheat, are not as familiar to the public as wheat (i.e. source of bread). Conversely, Kronenberger *et al.* (2014) compared perceptions toward various GE applications and found more concern when interspecies boundaries were crossed ('transgenics').

Sjöberg (2004) identified interfering with nature and severity of consequences as two of the most important dimensions of risk perceptions related to GE. Reproductive modification of forest trees might be viewed similarly, especially given the potential biodiversity impacts outlined earlier. Reproductive modification may be viewed as particularly unnatural because it represents a fundamental change to the natural process of procreation. This viewpoint has been emphasized by monikers such as 'terminator genes' in activism campaigns against reproductive modification technologies and their potential impacts on ownership of these technologies (Lombardo, 2014).

There have been only a few studies examining perceived risks associated with GE in trees. Tsourgiannis *et al.* (2016) compared consumer behaviors associated with GE paper products, woody biomass energy products and other wood products, and found that public safety issues and environmental impacts were among the largest concerns. Kazana *et al.* (2015, 2016) examined perceptions toward transgenic forest plantations and found that potential for gene escape causing contamination of wild forests (i.e. gene flow between transgenic plantation trees and wild trees) was the greatest perceived risk. Other concerns included susceptibility to disease from lignin content modification and impacts from higher herbicide inputs (i.e. from use of herbicide resistance traits). Lorentz & Minogue (2015) examined risks of eucalypt plantations and also found invasion potential and associated negative impacts on natural forests as primary concerns. These findings are consistent with Friedman & Foster (1997) who surveyed forest agency employees and found that loss of adaptation and genetic diversity, and changes in ecosystem components, were the largest perceived risks toward artificial regeneration in trees. Likewise, Needham *et al.* (2015) found that members of the public were most likely to agree that changing existing genes in trees and adding transgenes (from wheat or other distant species) will change the genetics of wild or native trees and cause long-term negative impacts that are currently unknown. Gene-flow risks, however, could be mitigated or avoided by the genetic containment mechanisms that are the focus of this paper. Thus, information and education about this new capability might affect risk perceptions.

Although risk perceptions dominate the literature, acceptance of reproductive modification also may be related to the extent that people view these applications as beneficial (e.g. high growth rates, control invasive species). Kazana *et al.* (2015, 2016) investigated perceptions of students (mostly European) toward GE trees in plantations and found that respondents perceived several benefits, including reductions in pesticide inputs, restoration of contaminated soils and higher tree productivity. These benefits, however, may differ based on the scale of production (e.g. plantation owners vs smaller community forests).

Knowledge and trust associated with GE Given the complexity of reproductive modification, most people are likely to be uninformed and lack knowledge about this topic. Yet, knowledge and awareness are often related to positive attitudes and acceptance of GE (James, 2004; Brossard & Nisbet, 2007; Huffman *et al.*, 2007; Connor & Siegrist, 2010). In the context of transgenic trees, Kazana *et al.* (2015) examined self-assessed knowledge and found that over 60% of students (mostly European) said they understood the meaning of transgenic trees and were willing to purchase GE products. However, fewer than half were aware of whether these trees could be deployed in plantation forestry (e.g. grown commercially, sold on the market). The investigators also believed there to be 'a serious perceived lack of knowledge about potential benefits and risks of the cultivation of transgenic forest trees' (Kazana *et al.*, 2015).

Given the technical nature of reproductive modification and likelihood that public knowledge about this topic is low, trust in knowledgeable experts (e.g. forest scientists, agencies) is an important consideration for understanding perceptions and acceptance. Trust is the willingness to rely on those responsible for making decisions or taking actions affecting public wellbeing (Siegrist, 2000). The public relies on trusted sources (e.g. scientists, agencies) to assess complex and unknown issues, and greater trust generally is associated with lower perceived risks, higher perceived benefits, more positive attitudes and higher acceptance (Siegrist, 2000; Siegrist & Cvetkovich, 2000). Sources such as agencies, companies and interest groups that are trusted by some people also can use information campaigns to influence perceptions and persuade people to support or oppose GE in various contexts (e.g. on private vs public land, plantations vs wild forests).

III. Synthesis

Although reproductive modification using GE may have benefits for productivity or containment of exotic species on its own, we consider that its primary use will be to facilitate the use of GE for other traits that would increase productivity, reduce losses to stressors, or improve wood-processing efficiency. Thus, an important question is whether benefits of GE are sufficient to offset the added costs to breeding of having sterile or partly sterile trees, and if economic costs of technology, regulatory approval and market limitations are sufficient to justify use of GE in general and reproductive modification in particular. Technology costs are considerable barriers, as many species and genotypes are difficult and costly to transform under present technology, further emphasizing the need for large benefits to justify GE. However, most published studies of the benefits of GE have only been of small-scale field studies of a few genotypes under highly controlled conditions, and the strong market-based preclusions to field studies make it unlikely there will be significant new, large-scale public research in the near future (Strauss *et al.*, 2015). GE, therefore, is likely to remain very limited in scale, potentially enabling considerable research on the ecological impacts of reproductive modification and other GE traits before their possible large-scale use.

1. Land sharing vs sparing

Conservation biologists are increasingly debating the benefits of land sparing (high-yielding agriculture on small land area) or land sharing (low-yielding wildlife-friendly agriculture covering more land) (Kremen, 2015; Phalan *et al.*, 2016). GE tree plantations have the potential to provide considerable production benefits, and such innovations are akin to developments that have occurred since the beginning of the agricultural revolution, which enabled high levels of food production on small land areas. However, those innovations resulted in large changes to the genetic composition of wild relatives of crops in many areas, as well as large reductions of general biological and genetic diversity within what became farms; similar potential changes via GE appear to be less acceptable today, presumably due to it being viewed as a more artificial process or the lack of knowledge on how prior innovations arose and have benefitted humanity. Central to the debate about whether GE plantations will provide indirect conservation benefits is whether growing more trees per unit area will ultimately result in more land set aside for conservation. Interestingly, there appears to be only a weak tendency for increased crop productivity to translate into higher rates of nature conservation in agricultural systems (Ewers *et al.*, 2009). Improved crop-growing efficiencies likely decrease per unit production costs, which could boost demand and provide further incentives for agricultural expansion into previously undeveloped areas. Thus, intensification needs to be coupled with 'strong governance' or zoning that requires parallel land conservation efforts (Kremen, 2015). Zoning approaches are not new to forest management. Seymour *et al.* (1999) proposed 'triad' methods where a forested land base is divided into three zones: intensively managed, extensively managed and protected areas. Several modeling exercises have explored the 'optimal' relative proportions of these zones (e.g. MacLean *et al.*, 2009; Ward & Erdle, 2015), but clearly such decisions will depend greatly on the forest type and biodiversity goals under consideration, as well as the relevant political, social and economic contexts.

With respect to GE plantations, optimal amounts of different management types will depend greatly on the amount and configuration of habitat required by native species, as well as whether they are capable of moving through and/or breeding in GE plantations with reproductive modification. In addition, the large structural and species changes within the intensively modified plantation systems where GE is likely to be most used are, in general, already complete or underway, and have already had large impacts on reproductive resources – with or without GE added. To the extent that such systems are already part of intentional or unintentional ‘triad’ systems to support biodiversity will to a large extent determine whether the added impacts of reproductive or other GE modifications are judged to have significant additional biological impacts. Such ‘zoning’ systems are commonly in place in many areas due to government controls on land uses or market-based controls such as from forest certification systems.

2. How should the Precautionary Principle be applied?

At first glance, following the ‘Precautionary Principle’ to biodiversity conservation would seem to necessarily require limited implementation of GE plantations, including those with modified reproduction. However, if this technology results in reduced land area required for wood production, or increased economic efficiency with spin-off benefits for society and environment – as has been argued forest plantations have done in many places, and that field trial experience with GE trees suggest could likely be delivered (discussed above) – application of the Precautionary Principle is by no means straightforward. As demand for wood products continues to expand, the risk of not using GE may come in form of increased rates of harvest in primary forest, conversion of native forests into non-GE plantations, and increased impacts to wild and planted forests from climate change-associated abiotic and biotic stressors. Thus failing to develop GE options could be viewed as being in opposition to the Precautionary Principle (Strauss, 2015). It is therefore critical that future policy decisions on GE be informed by the full suite of trade-offs between traditional forestry practices and implementation of GE plantations. Understanding the trade-offs, of course, requires continued research, both of GE benefits and biodiversity impacts. Unfortunately, both types of research have become difficult as a result of regulation and market obstacles (primarily forest certification systems) to field plantings (Strauss *et al.*, 2015). This preclusion is unfortunate as certification systems, such as PEFC, point to a lack of adequate research on GE trees as a reason for their exclusion: ‘... as the scientific evidence of potential benefits and dangers of genetically modified organisms (GMOs) and its impact on biodiversity remains insufficient and the society has not completed its debate, the PEFC General Assembly has determined that GMO cannot be considered as part of PEFC certified material’ (PEFC International, 2016). A critique of the Forest Stewardship Council’s GE policy, which was the first to ban all planted GE trees with no exemption for research, was first published in 2001 (Strauss *et al.*, 2001).

IV. Research priorities

There are a number of research avenues to improve understanding of the possible paths and impacts of reproductive modification in plantation trees. A few of the highest priority needs are briefly discussed below. A full list is provided in Notes S3.

1. GE reproductive modification

Both the science and technology underlying GE forestry is in its infancy; basic genetic and genomic science on which GE is based continue to expand rapidly. Perhaps the most promising path to new and more effective methods for reproductive modification is through direct gene editing, such as by the CRISPR-Cas system, which can be used for mutating genes required for male and/or female reproduction, and can be reversed if needed for further breeding. Such mutations should be highly if not perfectly stable, and after initial research to establish efficacy, can be identified and selected (based on rapid DNA analysis) years before natural flowering occurs (i.e. as soon as GE shoots are produced in the laboratory). Trees with desired changes can undergo accelerated flowering studies of their effects in the laboratory (e.g. using *FT* gene overexpression technology; Klocko *et al.*, 2014) followed by field studies of their impacts on reproductive and vegetative development. These studies should test for possible off-target effects and instability, improve delivery and removal methods, and monitor for pleiotropic effects on tree growth and development. Among the target genes should be those that are active late in reproduction, such as those required only during pollen germination and embryo development. In theory, knock-outs of the latter types may produce flowers, and even fruits and seeds, that can serve as normal resources for organisms that feed on them.

2. Biodiversity

Our literature searches have revealed an absence of studies directly addressing the effects of reproductive modification on plantation biodiversity. Thus, the most urgent need is for field sampling and experimental perturbations to analyze the extent of use, and dependence of plantation biota, on reproductive structures. This knowledge is needed for informing the design of hypothesis-driven stand and landscape-level experiments, and models of what landscape impacts might be and how they could be mitigated. It is also needed to help interpret the biological and social significance, and trade-offs, associated with reproductive modification compared to the many other human impacts on biological diversity. By understanding effects on biodiversity, this information also will provide insight into other ecosystem services that may be altered. Given there are so few GE plantations established around the world – and no species commercialized with reproductive modification – there appears to be ample time for surveys and experiments to inform management should social and political conditions become conducive to wider use of GE plantations.

3. Social dimensions

If reproductive modification is to be used for managing gene flow from GE and exotic plantations, it will be essential to understand what drives public attitudes and perceptions of benefits and risks. It also will be important to understand how reproductive modification is perceived by different stakeholders (e.g. public, experts, NGOs), as gene flow is itself a major concern voiced by opponents of GE in forestry. An important element of acceptance is likely to be familiarity. Given scientific uncertainty around reproductive modification, fear of unknown potential impacts will likely continue until science can shed light on these impacts and effectively communicate them in the context of other impacts on biodiversity (e.g. from agriculture, urbanization, plantations) and similar types of common technological interventions (e.g. neutering pets, birth control, seedless fruits, GE foods). Investigating benefits and costs of GE in forest plantations also will require ethical and political considerations such as how much biotechnology is needed, who makes final decisions and who takes responsibility.

V. Conclusion

Existing and developing genetic engineering (GE) technologies appear to be able to provide solutions to the problem of gene flow from GE and exotic plantation forests. However, there is little biological or social science research to inform about its impacts, the scale(s) at which it may become a concern, its significance in relation to other major sources of biodiversity perturbations, or the options for mitigation in the diverse species and coupled forest–human ecosystems where they might be applied. There are numerous opportunities for research to improve and extend GE technologies, and to fill gaps in knowledge of biodiversity impacts, but constraints in the form of market and regulatory restrictions to field research – and associated disinvestments in research from companies and governments – may make it difficult to fill these gaps in the foreseeable future.

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References

Abdullah ZS, Ficken KJ, Greenfield BPJ, Butt TM. 2014. Innate responses to putative ancestral hosts: is the attraction of Western Flower Thrips to pine pollen a result of relict olfactory receptors?. *Journal of Chemical Ecology* **40**: 534–540.

Alfaro-Sánchez R, Camarero JJ, López-Serrano FR, Sánchez-Salguero R, Moya D, Heras JDL. 2015. Positive coupling between growth and reproduction in young post-fire Aleppo pines depends on climate and site conditions. *International Journal of Wildland Fire* **24**: 507–517.

Allen RM. 1953. Release and fertilization stimulate longleaf pine cone crop. *Journal of Forestry* **51**: 172.

Andrén H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* **71**: 355–366.

Angelella GM, Riley DG. 2010. Effects of pine pollen supplementation in an onion diet on *Frankliniella fusca* reproduction. *Environmental Entomology* **39**: 505–512.

Araneda X, Caniullan R, Catalán C, Martínez M, Morales D, Rodríguez M. 2015. Aporte nutricional de polen de especies polinizadas por abejas (*Apis mellifera* L.) en la Región de La Araucanía, Chile. *Revista de la Facultad de Ciencias Agrarias, Universidad Nacional de Cuyo* **47**: 139–144.

Arien Y, Dag A, Zarchin S, Masci T, Shafir S. 2015. Omega-3 deficiency impairs honey bee learning. *Proceedings of the National Academy of Sciences, USA* **112**: 15 761–15 766.

Arista M, Talavera S (Sevilla U (Espana)). 1995. Cone production and cone crop pattern in *Abies pinsapo* Boiss. *Anales del Jardin Botanico de Madrid (Espana)* **53**: 5–12.

Arno SF, Hammerly R. 1977. *Northwest trees.* Seattle, WA, USA: Mountaineers Books.

Asaro C, Loeb SC, Hanula JL. 2003. Cone consumption by southeastern fox squirrels: a potential basis for clonal preferences in a loblolly and slash pine seed orchard. *Forest Ecology and Management* **186**: 185–195.

Ault K, Viswanath V, Jayawickrama J, Ma C, Eaton J, Meilan R, Beauchamp G, Hohenschuh W, Murthy G, Strauss SH. 2016. Improved growth and weed control of glyphosate-tolerant poplars. *New Forests* **47**: 653–667.

Ayari A, Khouja ML. 2014. Ecophysiological variables influencing Aleppo pine seed and cone production: a review. *Tree Physiology* **34**: 426–437.

Ayari A, Zubizarreta-Gerendiain A, Tome M, Tome J, Garchi S, Henchi B. 2012. Stand, tree and crown variables affecting cone crop and seed yield of Aleppo pine forests in different bioclimatic regions of Tunisia. *Forest Systems* **21**: 128–140.

Bardwell E, Benkman CW, Gould WR. 2001. Adaptive geographic variation in Western Scrub-Jays. *Ecology* **82**: 2617.

Barnes BV. 1969. *Effects of thinning and fertilizing on production of western white pine seed.* Ogden, UT, USA: US Department of Agriculture, Forest Service, Intermountain Research Station.

Barnett JP, Haugen RO. 1995. *Producing seed crops to naturally regenerate southern pines.* New Orleans, LA, USA: US Department of Agriculture, Forest Service, Southern Forest Experiment Station.

Barringer LE, Tomback DF, Wunder MB, McKinney ST. 2012. Whitebark pine stand condition, tree abundance, and cone production as predictors of visitation by Clark's Nutcracker. *PLoS ONE* **7**: e37663.

Bascompte J, Jordano P, Melián CJ, Olesen JM. 2003. The nested assembly of plant–animal mutualistic networks. *Proceedings of the National Academy of Sciences, USA* **100**: 9383–9387.

Becker CD, Boutin S, Larsen KW. 1998. Constraints on first reproduction in North American Red Squirrels. *Oikos* **81**: 81.

Behnke K, Grote R, Brüggemann N, Zimmer I, Zhou G, Elobeid M, Janz D, Polle A, Schnitzler J-P. 2012. Isoprene emission-free poplars – a chance to reduce the impact from poplar plantations on the atmosphere. *New Phytologist* **194**: 70–82.

Bellocq MI, Smith SM. 1994. Predation and overwintering mortality of the white pine weevil, Pissodesstrobi, in planted and seeded jack pine. *Canadian Journal of Forest Research* **24**: 1426–1433.

Benkman CW. 1993. Adaptation to single resources and the evolution of Crossbill (*Loxia*) diversity. *Ecological Monographs* **63**: 305–325.

Benkman CW. 2010. Diversifying coevolution between crossbills and conifers. *Evolution: Education and Outreach* **3**: 47–53.

Benkman CW, Parchman TL. 2009. Coevolution between crossbills and black pine: the importance of competitors, forest area and resource stability. *Journal of Evolutionary Biology* **22**: 942–953.

Bennett JM, Clarke RH, Thomson JR, Mac Nally R. 2014. Variation in abundance of nectarivorous birds: does a competitive despot interfere with flower tracking? *Journal of Animal Ecology* **83**: 1531–1541.

Betts MG, Forbes GJ, Diamond AW. 2007. Thresholds in songbird occurrence in relation to landscape structure. *Conservation Biology* **21**: 1046–1058.

Blancke S, Van Breusegem F, De Jaeger G, Braeckman J, Van Montagu M. 2015. Fatal attraction: the intuitive appeal of GMO opposition. *Trends in Plant Science* **20**: 414–418.

Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* **320**: 1444–1449.

Bonner FT, Karrfalt RP, eds. 2008. *The woody plant seed manual. Agriculture Handbook No. 727.* Washington, DC, USA: US Department of Agriculture, Forest Service.

Bremer LL, Farley KA. 2010. Does plantation forestry restore biodiversity or create green deserts? A synthesis of the effects of land-use transitions on plant species richness. *Biodiversity and Conservation* **19**: 3893–3915.

Briggs JS, Wall SBV, Jenkins SH. 2009. Forest rodents provide directed dispersal of Jeffrey Pine seeds. *Ecology* **90**: 675–687.

Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J. 2008. Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation* **17**: 925–951.

Brossard D, Nisbet MC. 2007. Deference to scientific authority among a low information public: understanding U.S. opinion on agricultural biotechnology. *International Journal of Public Opinion Research* **19**: 24–52.

Brunner AM, Li J, DiFazio SP, Shevchenko O, Montgomery BE, Mohamed R, Wei H, Ma C, Elias AA, VanWormer K *et al.* 2007. Genetic containment of forest plantations. *Tree Genetics & Genomes* **3**: 75–100.

Brzeziński M. 1994. Summer diet of the sable Martes zibellina in the Middle Yenisei taiga, Siberia. *Acta Theriologica* **39**: 103–107.

Calviño-Cancela M, Neumann M. 2015. Ecological integration of eucalypts in Europe: interactions with flower-visiting birds. *Forest Ecology and Management* **358**: 174–179.

Calviño-Cancela M, Rubido-Bará M. 2013. Invasive potential of *Eucalyptus globulus*: seed dispersal, seedling recruitment and survival in habitats surrounding plantations. *Forest Ecology and Management* **305**: 129–137.

Cecere JG, Cornara L, Mezzetta S, Ferri A, Spina F, Boitani L. 2011. Pollen couriers across the Mediterranean: the case of migrating warblers. *Ardea* **99**: 33–42.

Chen F, Chen J. 2011. Dispersal syndrome differentiation of *Pinus armandii* in Southwest China: key elements of a potential selection mosaic. *Acta Oecologica* **37**: 587–593.

Cho Y-J, Kim IS, Kim P, Lee EJ. 2003. Deposition of airborne pine pollen in a temperate pine forest. *Grana* **42**: 178–182.

Christensen KM, Whitham TG. 1993. Impact of insect herbivores on competition between birds and mammals for Pinyon pine seeds. *Ecology* **74**: 2270–2278.

Coleman HD, Cánovas FM, Man H, Kirby EG, Mansfield SD. 2012. Enhanced expression of glutamine synthetase (GS1a) confers altered fibre and wood chemistry in field grown hybrid poplar (*Populus tremula* × *alba*) (717-1B4). *Plant Biotechnology Journal* **10**: 883–889.

Connor M, Siegrist M. 2010. Factors influencing people's acceptance of gene technology: the role of knowledge, health expectations, naturalness, and social trust. *Science Communication* **32**: 514–538.

Cooper RW, Perry JH. 1956. Slash pine seeding habits. *Southern Lumberman* **193**: 198–199.

Copes DL, Bordelon M. 1994. Effects of tree spacing and height reduction on cone production in two Douglas-fir seed orchards. *Western Journal of Applied Forestry* **9**: 5–7.

Costa MA, Marques JV, Dalisay DS, Herman B, Bedgar DL, Davin LB, Lewis NG. 2013. Transgenic hybrid poplar for sustainable and scalable production of the commodity/specialty chemical, 2-phenylethanol. *PLoS ONE* **8**: e83169.

Costa-Font M, Gil JM, Traill WB. 2008. Consumer acceptance, valuation of and attitudes towards genetically modified food: review and implications for food policy. *Food Policy* **33**: 99–111.

Costello CM, van Manen FT, Haroldson MA, Ebinger MR, Cain SL, Gunther KA, Bjornlie DD. 2014. Influence of whitebark pine decline on fall habitat use and movements of grizzly bears in the Greater Yellowstone Ecosystem. *Ecology and Evolution* **4**: 2004–2018.

Croker TC. 1952. *Early release stimulates cone production. Southern Forestry Notes 79.* New Orleans, LA, USA: US Department of Agriculture, Forest Service, Southern Forest Experimental Station

Czechowski W, Marko B, Radchenko A. 2008. Rubbish dumps reveal the diet of ant colonies: *Myrmica schencki* Em. and *Myrmica rubra* (L.) Hymenoptera: Formicidae as facultative pollen eaters. *Polish Journal of Ecology* **56**: 737–741.

Davison A, Barns I, Schibeci R. 1997. Problematic publics: a critical review of surveys of public attitudes to biotechnology. *Science, Technology & Human Values* **22**: 317–348.

De Smet I, Lau S, Voss U, Vanneste S, Benjamins R, Rademacher EH, Schlereth A, De Rybel B, Vassileva V, Grunewald W *et al.* 2010. Bimodular auxin response controls organogenesis in Arabidopsis. *Proceedings of the National Academy of Sciences, USA* **107**: 2705–2710.

Després VR, Huffman JA, Burrows SM, Hoose C, Safatov AS, Buryak G, Fröhlich-Nowoisky J, Elbert W, Andreae MO, Pöschl U *et al.* 2012. Primary biological aerosol particles in the atmosphere: a review. *Tellus Series B* **64**: 3–40.

DiFazio SP. 2002. *Measuring and modeling gene flow from hybrid poplar plantations: implications for transgenic risk assessment.* PhD thesis, Oregon State University, Corvallis, OR, USA.

DiFazio SP, Leonardi S, Slavov GT, Garman SL, Adams WT, Strauss SH. 2012. Gene flow and simulation of transgene dispersal from hybrid poplr plantations. *New Phytologist* **193**: 903–915.

Dobson M, Goldingay RL, Sharpe DJ. 2005. Feeding behaviour of the squirrel glider in remnant habitat in Brisbane. *Australian Mammalogy* **27**: 27–35.

Dormont L, Roques A. 1999. A survey of insects attacking seed cones of *Pinus cembra* in the Alps, the Pyrenees and Massif Central. *Journal of Applied Entomology* **123**: 65–72.

Elias AA, Busov VB, Kosola KR, Ma C, Etherington E, Shevchenko O, Gandhi H, Pearce DW, Rood SB, Strauss SH. 2012. Green revolution trees: semidwarfism transgenes modify gibberellins, promote root growth, enhance morphological diversity, and reduce competitiveness in hybrid poplar. *Plant Physiology* **160**: 1130–1144.

Elias S, Witham J, Hunter M. 2006. A cyclic red-backed vole (*Clethrionomys gapperi*) population and seedfall over 22 years in maine. *Oxford Journals* **87**: 440–445.

Elorriaga E, Klocko AL, Ma C, Strauss SH. 2015. *CRISPR-Cas nuclease mutagenesis for genetic containment of genetically engineered forest trees.* PowerPoint Presentation – Elorriaga_poster_PlantBiology2015v3a.pdf.

Elorriaga E, Meilan R, Ma C, Skinner JS, Etherington E, Brunner A, Strauss SH. 2014. A tapetal ablation transgene induces stable male sterility and slows field growth in *Populus*. *Tree Genetics & Genomes* **10**: 1583–1593.

Espelta JM, Verkaik I. 2007. Effect of thinning and postfire regeneration age on growth and reproductive traits of *Pinus halepensis* forests. In: Leone V, Lovreglio R, eds, *Proceedings of the international workshop MEDPINE 3: conservation, regeneration and restoration of Mediterranean pines and their ecosystems*. Bari, Italy: CIHEAM, 2007, 93–97 [WWW document] URL http://ressources.ciheam.org/om/pdf/a75/00800319.pdf [accessed 21 December 2016].

Ewers RM, Scharlemann JPW, Balmford A, Green RE. 2009. Do increases in agricultural yield spare land for nature? *Global Change Biology* **15**: 1716–1726.

Fahrig L. 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* **105**: 273–292.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics* **34**: 487–515.

FAO. 2010. *Forests and genetically modified trees.* Rome, Italy: FAO.

FAO, WFP, IFAD. 2012. *The state of food insecurity in the world 2012: Economic growth is necessary but not sufficient to accelerate reduction of hunger and malnutrition.* Rome, Italy: FAO.

Finucane ML, Holup JL. 2005. Psychosocial and cultural factors affecting the perceived risk of genetically modified food: an overview of the literature. *Social Science & Medicine* **60**: 1603–1612.

Fishbein M, Ajzen I. 2010. *Predicting and changing behavior: the reasoned action approach.* New York, USA: Psychology Press.

Fletcher RJ Jr. 2006. Emergent properties of conspecific attraction in fragmented landscapes. *The American Naturalist* **168**: 207–219.

Florence RG, McWilliam JR. 1954. Observations on the dispersion of pollen from a slash pine plantation: its possible effect in contaminating a slash pine seed orchard. *Queensland Forest Service Research Note* **5**: 7.

Fowells HA. 1965. *Silvics of forest trees of the United States. Agriculture handbook.* Washington, DC, USA: US Department of Agriculture.

Franke R, McMichael CM, Meyer K, Shirley AM, Cusumano JC, Chapple C. 2000. Modified lignin in tobacco and poplar plants over-expressing the Arabidopsis gene encoding ferulate 5-hydroxylase. *Plant Journal: for Cell and Molecular Biology* **22**: 223–234.

Frewer L, Lassen J, Kettlitz B, Scholderer J, Beekman V, Berdal KG. 2004. Societal aspects of genetically modified foods. *Food and Chemical Toxicology* **42**: 1181–1193.

Frewer LJ, Scholderer J, Bredahl L. 2003. Communicating about the risks and benefits of genetically modified foods: the mediating role of trust. *Risk Analysis: An Official Publication of the Society for Risk Analysis* **23**: 1117–1133.

Friedman ST, Foster GS. 1997. Forest genetics on federal lands in the United States: public concerns and policy responses. *Canadian Journal of Forest Research* **27**: 401–408.

Gamfeldt L, Snäll T, Bagchi R, Jonsson M, Gustafsson L, Kjellander P, Ruiz-Jaen MC, Fröberg M, Stendahl J, Philipson CD *et al.* 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. *Nature Communications* 4: 1340.

Garcia-del-Rey E, Nanos N, López-de-Heredia U, Muñoz PG, Otto R, Fernández-Palacios JM, Gil L. 2011. Spatiotemporal variation of a *Pinus* seed rain available for an endemic finch in an insular environment. *European Journal of Wildlife Research* 57: 337–347.

Gashwiler JS. 1970. Further study of conifer seed survival in a Western Oregon clearcut. *Ecology* 51: 849–854.

Gautier-Hion A, Duplantier J-M, Quris R, Feer F, Sourd C, Decoux J-P, Dubost G, Emmons L, Erard C, Hecketsweiler P *et al.* 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324–337.

Goubitz S, Nathan R, Roitemberg R, Shmida A, Ne'eman G. 2004. Canopy seed bank structure in relation to: fire, tree size and density. *Plant Ecology* 173: 191–201.

Graham MD, Vinebrooke RD, Turner MA. 2006. Coupling of boreal forests and lakes: effects of conifer pollen on littoral communities. *Limnology and Oceanography* 51: 1524–1529.

Grano CX. 1970. *Seed yields in Loblolly-Shortleaf Pine selection stands.* New Orleans, LA, USA: US Department of Agriculture, Forest Service, Southern Forest Experimental Station.

Grayson KJ, Wittwer RF, Shelton MG. 2002. *Cone characteristics and seed quality 10 years after an uneven-aged regeneration cut in shortleaf pine stands.* Gen. Tech. Rep. SRS–48. Asheville, NC, USA: US Department of Agriculture, Forest Service, Southern Research Station, 310–314

Griffin AR, Hingston AB, Ohmart CP. 2009. Pollinators of *Eucalyptus regnans* (Myrtaceae), the world's tallest flowering plant species. *Australian Journal of Botany* 57: 18.

de Groot P, DeBarr GL. 1998. Factors affecting capture of the white pine cone beetle, *Conophthorus coniperda* (Schwarz)(Col., Scolytidae) in pheromone traps. *Journal of Applied Entomology* 122: 281–286.

Guglielmo CG, Karasov WH. 1995. Nutritional quality of winter browse for Ruffed Grouse. *The Journal of Wildlife Management* 59: 427–436.

Gunther KA, Shoemaker RR, Frey KL, Haroldson MA, Cain SL, van Manen FT, Fortin JK. 2014. Dietary breadth of grizzly bears in the Greater Yellowstone Ecosystem. *Ursus* 25: 60–72.

Gupta N, Fischer ARH, Frewer LJ. 2011. Socio-psychological determinants of public acceptance of technologies: a review. *Public Understanding of Science* 21: 782–795.

Guries R, Stevens D, Peterson K. 2010. *Wisconsin Forest Tree Improvement Program 2010 annual report.* Madison, WI, USA: Wisconsin Department of Natural Resources.

Haddad NM, Tewksbury JJ. 2005. Low-quality habitat corridors as movement conduits for two butterfly species. *Ecological Applications* 15: 250–257.

Häggman H, Raybould A, Borem A, Fox T, Handley L, Hertzberg M, Lu M-Z, Macdonald P, Oguchi T, Pasquali G *et al.* 2013. Genetically engineered trees for plantation forests: key considerations for environmental risk assessment. *Plant Biotechnology Journal* 11: 785–798.

Halls LK, Hawley NR. 1954. *Slash pine cone production is increased by seed-tree release.* Asheville, NC: US Department of Agriculture, Forest Service, Southeastern Forest Experiment Station, Research note 66.

Hamer D, Pengelly I. 2015. Whitebark Pine (*Pinus albicaulis*) seeds as food for bears (*Ursus* spp.) in Banff National Park, Alberta. *The Canadian Field-Naturalist* 129: 8–14.

Hanski I. 1998. Metapopulation dynamics. *Nature* 396: 41–49.

Hilgert-Moreira SB, Nascher CA, Callegari-Jacques SM, Blochtein B. 2014. Pollen resources and trophic niche breadth of *Apis mellifera* and *Melipona obscurior* (Hymenoptera, Apidae) in a subtropical climate in the Atlantic rain forest of southern Brazil. *Apidologie* 45: 129–141.

Hingston AB, Potts BM. 2005. Pollinator activity can explain variation in outcrossing rates within individual trees. *Austral Ecology* 30: 319–324.

Hingston AB, Potts BM, McQuillan P. 2004a. Pollination services provided by various size classes of flower visitors to *Eucalyptus globulus* ssp. *globulus* (Myrtaceae). *Australian Journal of Botany* 52: 353–369.

Hingston AB, McQuillan PB, Potts BM. 2004b. Pollinators in seed orchards of Eucalyptus nitens (Myrtaceae). *Australian Journal of Botany* 52: 209–222.

Hollander JL, Vander Wall SB. 2004. Effectiveness of six species of rodents as dispersers of singleleaf piñon pine (*Pinus monophylla*). *Oecologia* 138: 57–65.

Howe H, Smallwood J. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.

Hu JJ, Tian YC, Han YF, Li L, Zhang BE. 2001. Field evaluation of insect-resistant transgenic *Populus nigra*. *Euphytica* 121: 123–127.

Huffman WE, Rousu M, Shogren JF, Tegene A. 2007. The effects of prior beliefs and learning on consumers' acceptance of genetically modified foods. *Journal of Economic Behavior & Organization* 63: 193–206.

Hutchison LJ, Barron GL. 1997. Parasitism of pollen as a nutritional source for lignicolous Basidiomycota and other fungi. *Mycological Research* 101: 191–194.

Invernizzi C, Rivas F, Bettucci L. 2011. Resistance to Chalkbrood Disease in *Apis mellifera* L. (Hymenoptera: Apidae) colonies with different hygienic behaviour. *Neotropical Entomology* 40: 28–34.

Irwin RE, Bronstein JL, Manson JS, Richardson L. 2010. Nectar robbing: ecological and evolutionary perspectives. *Annual Review of Ecology, Evolution, and Systematics* 41: 271–292.

Jakubas WJ, Karasov WH, Guglielmo CG. 1993. Coniferyl benzoate in Quaking Aspen (*Populus tremuloides*): its effect on energy and nitrogen digestion and retention in Ruffed Grouse (*Bonasa umbellus*). *Physiological Zoology* 66: 580–601.

James JS. 2004. Consumer knowledge and acceptance of agricultural biotechnology vary. *California Agriculture* 58: 99–105.

Jing ZP, Gallardo F, Pascual MB, Sampalo R, Romero J, De Navarra AT, Cánovas FM. 2004. Improved growth in a field trial of transgenic hybrid poplar overexpressing glutamine synthetase. *New Phytologist* 164: 137–145.

Johnson M, Vander Wall SB, Borchert M. 2003. A comparative analysis of seed and cone characteristics and seed-dispersal strategies of three pines in the subsection Sabinianae. *Plant Ecology* 168: 69–84.

Kazana V, Tsourgiannis L, Iakovoglou V, Stamatiou C, Alexandrov A, Araújo S, Bogdan S, Bozic G, Brus R, Bossinger G *et al.* 2015. Public attitudes towards the use of transgenic forest trees: a cross-country pilot survey. *iForest - Biogeosciences and Forestry* 9: 344.

Kazana V, Tsourgiannis L, Iakovoglou V, Stamatiou C, Alexandrov A, Araújo S, Bogdan S, Božič G, Brus R, Bossinger G *et al.* 2016. Public knowledge and perceptions of safety issues towards the use of genetically modified forest trees: a cross-country pilot survey. In: Vettori C, Gallardo F, Häggman H, Kazana V, Migliacci F, Pilate G, Fladung M, eds. *Biosafety of forest transgenic trees: improving the scientific basis for safe tree development and implementation of EU policy directives.* Dordrecht, the Netherlands: Springer, 223–244.

Klocko AL, Borejsza-Wysocka E, Brunner AM, Aldwinckle H, Strauss SH. 2016a. Transgenic suppression of AGAMOUS genes in apple reduces fertility and increases floral attractiveness. *PloS ONE* 11: e0159421.

Klocko AL, Brunner AM, Huang J, Meilan R, Lu H, Ma C, Morel A, Zhao D, Ault K, Dow M *et al.* 2016b. Containment of transgenic trees by suppression of LEAFY. *Nature Biotechnology* 34: 918–922.

Klocko AL, Etherington E, Ault K, Brunner AM, Lockwood T, Covarrubias N, Ma C, Manzhu B, Strauss SH. 2016c. *RNAi suppression of two AGAMOUS homologs in sweetgum (Liquidambar) impairs male and female reproductive evelopment under field conditions.* Corvallis, OR, USA: Poster, Oregon State University. [WWW document] URL http://people.forestry.oregonstate.edu/stevestrauss/sites/people.forestry.oregonstate.edu.steve-strauss/files/Klocko%20PAG%202016%20RNAi%20AG%20sweetgum%20v2b.pdf [accessed 21 December 2016].

Klocko AL, Meilan R, James RR, Viswanath V, Ma C, Payne P, Miller L, Skinner JS, Oppert B, Cardineau GA *et al.* 2014. Bt-Cry3Aa transgene expression reduces insect damage and improves growth in field-grown hybrid poplar. *Canadian Journal of Forest Research* 44: 28–35.

Koenig WD, Knops JMH. 1998. Scale of mast-seeding and tree-ring growth. *Nature* 396: 225–226.

Kozlowski TT, Kramer PJ, Pallardy SG. 2012. *The physiological ecology of woody plants.* San Diego, CA, USA: Academic Press.

Kremen C. 2015. Reframing the land-sparing/land-sharing debate for biodiversity conservation. *Annals of the New York Academy of Sciences* 1355: 52–76.

Kronberger N, Wagner W, Nagata M. 2014. How natural is "more natural"? The role of method, type of transfer, and familiarity for public perceptions of cisgenic and transgenic modification. *Science Communication* 36: 106–130.

Krugman SL, Jenkinson JL. 1974. *Pinus* L. Pine. In: Schopmeyer CS, tech. coord. *Seeds of woody plants in the United States*. Washington, DC: US Department of Agriculture, Agriculture Handbook 450, 598–638

Kuhn KM, Vander Wall SB. 2007. Black bears (*Ursus americanus*) harvest Jeffrey Pine (*Pinus jeffreyi*) seeds from tree canopies. *Western North American Naturalist* **67**: 384–388.

Labandeira CC, Eble GJ. 2000. *The fossil record of insect diversity and disparity*. Johannesburg, South Africa: Witwatersrand University Press.

Leatherman D. 2011. Dorytomus weevil larvae in cottonwood catkins. *Colorado Birds* **45**: 124–127.

Leveau LM, Leveau CM. 2011. Nectarivorous feeding by the Bay-winged Cowbird (*Agelaioides badius*). *Studies on Neotropical Fauna and Environment* **46**: 173–175.

Li J, Brunner AM, Shevchenko O, Meilan R, Ma C, Skinner JS, Strauss SH. 2008. Efficient and stable transgene suppression via RNAi in field-grown poplars. *Transgenic Research* **17**: 679–694.

Lindroth RL, St Clair SB. 2013. Adaptations of quaking aspen (*Populus tremuloides* Michx.) for defense against herbivores. *Forest Ecology and Management* **299**: 14–21.

Lombardo L. 2014. Genetic use restriction technologies: a review. *Plant Biotechnology Journal* **12**: 995–1005.

Lorentz KA, Minogue PJ. 2015. Exotic Eucalyptus plantations in the southeastern US: Risk assessment, management and policy approaches. *Biological Invasions* **17**: 1581–1593.

Lu H, Viswanath V, Ma C, Etherington E, Dharmawardhana P, Shevchenko O, Strauss SH, Pearce DW, Rood SB, Busov V. 2015. Recombinant DNA modification of gibberellin metabolism alters growth rate and biomass allocation in *Populus*. *Tree Genetics & Genomes* **11**: 1–16.

Lu N, Wei B, Sun Y, Liu X, Chen S, Zhang W, Zhang Y, Li Y. 2014. Field supervisory test of DREB-transgenic *Populus*: salt tolerance, long-term gene stability and horizontal gene transfer. *Forests* **5**: 1106–1121.

Lucht JM. 2015. Public acceptance of plant biotechnology and GM crops. *Viruses* **7**: 4254–4281.

MacLean DA, Seymour RS, Montigny MK, Messier C. 2009. Allocation of conservation efforts over the landscape: the TRIAD approach. In: Villard M-A, (ed), *Setting conservation targets for managed forest landscapes*. Cambridge, UK: Cambridge University Press.

MacNally R, Horrocks G. 2000. Landscape-scale conservation of an endangered migrant: the Swift Parrot (*Lathamus discolor*) in its winter range. *Biological Conservation* **92**: 335–343.

Mailleux A-C, Furey R, Saffre F, Krafft B, Deneubourg J-L. 2008. How non-nestmates affect the cohesion of swarming groups in social spiders. *Insectes Sociaux* **55**: 355–359.

Małyska A, Maciąg K, Twardowski T. 2014. Perception of GMOs by scientists and practitioners – the critical role of information flow about transgenic organisms. *New Biotechnology* **31**: 196–202.

Mansfield SD, Kang K-Y, Chapple C. 2012. Designed for deconstruction – poplar trees altered in cell wall lignification improve the efficacy of bioethanol production. *New Phytologist* **194**: 91–101.

Marsden SJ, Pilgrim JD. 2003. Factors influencing the abundance of parrots and hornbills in pristine and disturbed forests on New Britain, PNG: parrot and hornbill abundances, New Britain, PNG. *Ibis* **145**: 45–53.

Marty B. 2015. 'Landless' women workers destroy GMO lab in Brazil. *PanAm Post*. [WWW document] URL https://panampost.com/belen-marty/2015/03/09/landless-women-workers-destroy-gmo-lab-in-brazil. [accessed 8 December 2016]

Masclaux H, Bec A, Kagami M, Perga M-E, Sime-Ngando T, Desvilettes C, Bourdier G. 2011. Food quality of anemophilous plant pollen for zooplankton. *Limnology and Oceanography* **56**: 939–946.

Maser C, Mate BR, Franklin JF, Dyrness CT. 1981. *Natural history of Oregon coast mammals*. Portland, OR, USA: US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Maynard CA, Powell WA, Polin-McGuigan LD, Viéitez AM, Ballester A, Corredoira E, Merkle SA, Andrade GM. 2009. *Chestnut. Compendium of transgenic crop plants*. Chichester, UK: John Wiley & Sons Ltd.

McCall AC, Irwin RE. 2006. Florivory: the intersection of pollination and herbivory. *Ecology Letters* **9**: 1351–1365.

McCartney J, Stringer IAN, Potter MA. 2007. Feeding activity in captive New Zealand lesser short-tailed bats (*Mystacina tuberculata*). *New Zealand Journal of Zoology* **34**: 227–238.

Meilan R, Han K-H, Ma C, DiFazio SP, Eaton JA, Hoien EA, Stanton BJ, Crockett RP, Taylor ML, James RR *et al.* 2002. The CP4transgene provides high levels of tolerance to Roundup® herbicide in field-grown hybrid poplars. *Canadian Journal of Forest Research* **32**: 967–976.

Menz MHM, Brown GR, Dixon KW, Phillips RD. 2015. Absence of nectar resource partitioning in a community of parasitoid wasps. *Journal of Insect Conservation* **19**: 703–711.

Mezquida ET, Benkman CW. 2005. The geographic selection mosaic for squirrels, crossbills and Aleppo pine: a geographic selection mosaic. *Journal of Evolutionary Biology* **18**: 348–357.

Mikich SB, Liebsch D. 2014. Damage to forest plantations by tufted capuchins (*Sapajus nigritus*): too many monkeys or not enough fruits? *Forest Ecology and Management* **314**: 9–16.

Miller DR, Crowe CM, Asaro C, Debarr GL. 2003. Dose and enantiospecific responses of white pine cone beetles, Conophthorus coniperda, to a-pinene in an eastern white pine seed orchard. *Journal of Chemical Ecology* **29**: 437–451.

Millar JG, Paine TD, Joyce AL, Hanks LM. 2003. The effects of *Eucalyptus* pollen on longevity and fecundity of *Eucalyptus* Longhorned Borers (Coleoptera: Cerambycidae). *Journal of Economic Entomology* **96**: 370–376.

Molinari A, Wauters LA, Airoldi G, Cerinotti F, Martinoli A, Tosi G. 2006. Cone selection by Eurasian red squirrels in mixed conifer forests in the Italian Alps. *Acta Oecologica* **30**: 1–10.

Moncur MW, Mitchell A, Fripp Y, Kleinschmidt GJ. 1995. The role of honey bees (*Apis mellifera*) in eucalypt and acacia seed production areas. *The Commonwealth Forestry Review* **74**: 350–354.

More S, Ghorai N, Bera S. 2010. Study on the selection of some local pollen plants in West Bengal, India as pollen brood feed in *Apis cerana* Fabr. larvae by the worker bees, through meconia analysis and community ordination method of recovered pollen taxa. *Proceedings of the Zoological Society* **63**: 39–44.

Mound L. 1998. A peripatetic australian thrips (Thysanoptera: phlaeothriqidae) in eucalyptus seed capsules. *Australian Entomologist* **25**: 85–86.

Moya D, De las Heras J, López-Serrano FR, Condes S, Alberdi I. 2009. Structural patterns and biodiversity in burned and managed Aleppo Pine stands. *Plant Ecology* **200**: 217–228.

Moya D, De las Heras J, López-Serrano FR, Leone V. 2008. Optimal intensity and age of management in young Aleppo pine stands for post-fire resilience. *Forest Ecology and Management* **255**: 3270–3280.

Moya-Laraño J, Vinković D, Allard CM, Foellmer MW. 2007. Mass-mediated sex differences in climbing patterns support the gravity hypothesis of sexual size dimorphism. *Web Ecology* **7**: 106–112.

Munsell J, Fox T. 2010. An analysis of the feasibility for increasing woody biomass production from pine plantations in the southern United States. *Biomass and Bioenergy* **34**: 1631–1642.

Myczko Ł, Skórka P, Dylewski Ł, Sparks TH, Tryjanowski P. 2015. Color mimicry of empty seeds influences the probability of predation by birds. *Ecosphere* **6**: art177.

Needham M, Howe G, Petit J. 2015. *Forest health biotechnologies: What are the drivers of public acceptance?* Washington, DC, USA: Forest Health Initiative Annual Meeting. [WWW document] URL http://foresthealthinitiative.org/resources/Needham2015.pdf [accessed 8 December 2016].

Newhouse AE, Schrodt F, Liang H, Maynard CA, Powell WA. 2007. Transgenic American elm shows reduced Dutch elm disease symptoms and normal mycorrhizal colonization. *Plant Cell Reports* **26**: 977–987.

Obregon D, Nates-Parra G. 2014. Floral preference of *Melipona eburnea* Friese (Hymenoptera: Apidae) in a Colombian Andean Region. *Neotropical Entomology* **43**: 53–60.

Oliveira-Abreu C, Hilário SD, Luz CFP, Alves dos Santos I. 2014. Pollen and nectar foraging by *Melipona quadrifasciata anthidioides* Lepeletier (Hymenoptera: Apidae: Meliponini) in natural habitat. *Sociobiology* **61**: 441–448.

Ottewell K, Dunlop J, Thomas N, Morris K, Coates D, Byrne M. 2014. Evaluating success of translocations in maintaining genetic diversity in a threatened mammal. *Biological Conservation* **171**: 209–219.

Pajoro A, Biewers S, Dougali E, Valentim FL, Mendes MA, Porri A, Coupland G, de Peer YV, van Dijk ADJ, Colombo L *et al.* 2014. The (r)evolution of gene regulatory networks controlling Arabidopsis plant reproduction: a two-decade history. *Journal of Experimental Botany* **65**: 4731–4745.

Parchman TL, Benkman CW. 2008. The geographic selection mosaic for ponderosa pine and crossbills: a tale of two squirrels. *Evolution* **62**: 348–360.

Parchman TL, Benkman CW, Britch SC. 2006. Patterns of genetic variation in the adaptive radiation of New World crossbills (Aves: *Loxia*): AFLP variation in crossbills. *Molecular Ecology* **15**: 1873–1887.

Pasonen H-L, Seppänen S-K, Degefu Y, Rytkönen A, von Weissenberg K, Pappinen A. 2004. Field performance of chitinase transgenic silver birches (*Betula pendula*): resistance to fungal diseases. *Theoretical and Applied Genetics* **109**: 562–570.

PEFC International. 2016. *Forest issues. Biodiversity.* [WWW document] URL http://www.pefc.org/forest-issues/sustainability/biodiversity [accessed 18 October 2016].

Perez-Moreno J, Read DJ. 2001. Exploitation of pollen by mycorrhizal mycelial systems with special reference to nutrient recycling in boreal forests. *Proceedings of the Royal Society B* **268**: 1329–1335.

Pernal S, Currie R. 2000. Pollen quality of fresh and 1-year-old single pollen diets for worker honey bees (*Apis mellifera* L.). *Apidologie* **31**: 387–409.

Petermann A. 2015. Corporate profit trumps common sense in Brazil. *New Internationalist.* [WWW document] URL https://newint.org/blog/2015/04/24/gm-trees-brazil [accessed 8 December 2016].

Phalan B, Green RE, Dicks LV, Dotta G, Feniuk C, Lamb A, Strassburg BBN, Williams DR, zu Ermgassen EKHJ, Balmford A. 2016. How can higher-yield farming help to spare nature? *Science* **351**: 450–451.

Phares R, Rogers N. 1962. Improving shortleaf pine direct seedling success affected by month of seedling, release method and weather. *Journal of Forestry* **60**: 322–324.

Pilate G, Guiney E, Holt K, Petit-Conil M, Lapierre C, Leplé J-C, Pollet B, Mila I, Webster EA, Marstorp HG *et al.* 2002. Field and pulping performances of transgenic trees with altered lignification. *Nature Biotechnology* **20**: 607–612.

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science (New York, N.Y.)* **344**: 1246752.

Podruzny S, Reinhart D, Mattson D. 1999. Fire, red squirrels, whitebark pine, and yellowstone grizzly bears. *Ursus* **11**: 131–138.

Pope FD. 2010. Pollen grains are efficient cloud condensation nuclei. *Environmental Research Letters* **5**: 44015.

Porth I, El-Kassaby Y. 2014. Current status of the development of genetically modified (GM) forest trees world-wide: a comparison with the development of other GM plants in agriculture. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources* **9**: 1–12.

Rastogi Verma S. 2013. Genetically modified plants: public and scientific perceptions. *International Scholarly Research Notices Biotechnology* **2013**: e820671.

Ricklefs RE. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**: 167–171.

Riley DG, Angelella GM, McPherson RM. 2011. Pine pollen dehiscence relative to thrips population dynamics: pine pollen and thrips population dynamics. *Entomologia Experimentalis et Applicata* **138**: 223–233.

Robinson SK, Thompson FR, Donovan TM, Whitehead DR, Faaborg J. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* **267**: 1987–1990.

Rong K, Yang H, Ma J, Zong C, Cai T. 2013. Food availability and animal space use both determine cache density of Eurasian Red Squirrels. *PLoS ONE* **8**: e80632.

Root HT, Betts MG. 2016. Managing moist temperate forests for bioenergy and biodiversity. *Journal of Forestry* **114**: 66–74.

Roulston TH, Cane JH. 2000. Pollen nutritional content and digestibility for animals. *Plant Systematics and Evolution* **222**: 187–209.

Ruano I, Manso R, Fortin M, Bravo F. 2015. Extreme climate conditions limit seed availability to successfully attain natural regeneration of *Pinus pinaster in* sandy areas of central Spain. *Canadian Journal of Forest Research* **45**: 1795–1802.

Rumble MA, Anderson SH. 1996. Microhabitats of Merriam's Turkeys in the Black Hills, South Dakota. *Ecological Applications* **6**: 326–334.

Sakai S, Harrison RD, Momose K, Kuraji K, Nagamasu H, Yasunari T, Chong L, Nakashizuka T. 2006. Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. *American Journal of Botany* **93**: 1134–1139.

Santangelo E, Assirelli A, Spinelli R, Pari L. 2016. A single-pass reduced tillage technique for the establishment of short-rotation poplar (*Populus* spp.) plantations. *Croatian Journal of Forest Engineering* **37**: 61–69.

Santos-del-Blanco L, Alía R, González-Martínez SC, Sampedro L, Lario F, Climent J. 2015. Correlated genetic effects on reproduction define a domestication syndrome in a forest tree. *Evolutionary Applications* **8**: 403–410.

Schlaepfer MA, Runge MC, Sherman PW. 2002. Ecological and evolutionary traps. *Trends in Ecology & Evolution* **17**: 474–480.

Schmidt KA, Johansson J, Betts MG. 2015. Information-mediated allee effects in breeding habitat selection. *The American Naturalist* **186**: E162–E171.

Schumaker NH, Ernst T, White D, Baker J, Haggerty P. 2004. Projecting wildlife responses to alternative future landscapes in Oregon's Willamette basin. *Ecological Applications* **14**: 381–400.

Shepherd KR. 1986. *Plantation silviculture.* Dordrecht, the Netherlands: Springer.

Sherif SM, Shukla MR, Murch SJ, Bernier L, Saxena PK. 2016. Simultaneous induction of jasmonic acid and disease-responsive genes signifies tolerance of American elm to Dutch elm disease. *Scientific Reports* **6**: 21934.

Siegrist M. 2000. The influence of trust and perceptions of risks and benefits on the acceptance of gene technology. *Risk Analysis* **20**: 195–204.

Siegrist M, Cvetkovich G. 2000. Perception of hazards: the role of social trust and knowledge. *Risk Analysis* **20**: 713–720.

Siepielski AM, Benkman CW. 2004. Interactions among moths, crossbills, squirrels, and lodgepole pine in a geographic selection mosaic. *Evolution* **58**: 95–101.

Siepielski AM, Benkman CW. 2007. Convergent patterns in the selection mosaic for two North American bird-dispersed pines. *Ecological Monographs* **77**: 203–220.

Simeão CMG, Silveira FA, Sampaio IBM, Bastos EMAF. 2015. Pollen analysis of honey and pollen collected by *Apis mellifera* Linnaeus, 1758 (Hymenoptera, Apidae), in a mixed environment of Eucalyptus plantation and native cerrado in Southeastern Brazil. *Brazilian Journal of Biology* **75**: 821–829.

Sivilov O, Atanassova J, Zlatkov B. 2011. Food plant spectrum of Oedemeridae species (Insecta, Coleoptera) based on pollen analysis (a preliminary study). *Comptes Rendus de l'Académie Bulgare des Sciences* **64**: 225–230.

Sjöberg L. 2004. Principles of risk perception applied to gene technology. *EMBO Reports* **5**: S47–S51.

Skolmen RG, Ledig TF. 1990. Eucalyptus globulus Labill. bluegum eucalyptus. In: Burns RM, Honkala BH, tech. coord., *Silvics of North America: vol. 2, Hardwoods. Agriculture handbook 654.* Washington, DC: US Department of Agriculture, Forest Service, 299–304.

Slovic P. 2000. *The perception of risk.* London, UK: Earthscan Publications.

Smith CC. 1970. The coevolution of Pine Squirrels (*Tamiasciurus*) and conifers. *Ecological Monographs* **40**: 349–371.

Snyder NF, Koenig SE, Koschmann J, Snyder HA, Johnson TB. 1994. Thick-billed parrot releases in Arizona. *Condor* **96**: 845–862.

Smith C, Balda R. 1979. Competition among insects, birds, and mammals for conifer seeds. *Oxford Journals* **19**: 1065–1083.

Steiner AL, Brooks SD, Deng C, Thornton DCO, Pendleton MW, Bryant V. 2015. Pollen as atmospheric cloud condensation nuclei. *Geophysical Research Letters* **42**: 2015GL064060.

Strauss SH. 2015. Biotech and forest health: creating a path for pragmatism. *The Forestry Source* **20**: 11.

Strauss SH, Campbell MM, Pryor SN, Coventry P, Burley J. 2001. Plantation certification and genetic engineering: FSC's ban on research is counterproductive. *Journal of Forestry* **99**: 4–7.

Strauss SH, Costanza A, Séguin A. 2015. Genetically engineered trees: paralysis from good intentions. *Science* **349**: 794–795.

Strauss SH, Rottmann WH, Brunner AM, Sheppard LA. 1995. Genetic engineering of reproductive sterility in forest trees. *Molecular Breeding* **1**: 5–26.

Strauss SH, Schmitt M, Sedjo R. 2009. Forest scientist views of regulatory obstacles to research and development of transgenic forest biotechnology. *Journal of Forestry* **107**: 350–357.

Strothmann RO, Roy DF. 1984. *Regeneration of Douglas-fir in the Klamath Mountains region, California and Oregon.* Berkeley, CA, USA: US Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station.

Summers RW. 2011. Patterns of exploitation of annually varying *Pinus sylvestris* cone crops by seed-eaters of differing dispersal ability. *Ecography* **34**: 723–728.

Summers RW, Proctor R. 1999. Tree and cone selection by crossbills *Loxia* sp. and red squirrels *Sciurus vulgaris* at Abernethy forest, Strathspey. *Forest Ecology and Management* **118**: 173–182.

Teste F, Liefers V, Landhausser S. 2011. Seed release in serotinous lodgepole pine forests after mountain pine beetle outbreak. *Ecological Society of America* **21**: 150–162.

van Tets IG, Hulbert AJ. 1999. A comparison of the nitrogen requirements of the Eastern Pygmy Possum, *Cercartetus nanus*, on a pollen and on a mealworm diet. *Physiological and Biochemical Zoology* **72**: 127–137.

Thayer TC, Vander Wall SB. 2005. Interactions between Steller's jays and yellow pine chipmunks over scatter-hoarded sugar pine seeds. *Journal of Animal Ecology* **74**: 365–374.

Tomback DF, Achuff P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. *Forest Pathology* **40**: 186–225.

Tomback DF, Linhart YB. 1990. The evolution of bird-dispersed pines. *Evolutionary Ecology* **4**: 185–219.

Trebra CV, Lavender DP, Sullivan TP. 1998. Relations of small mammal populations to even-aged shelterwood systems in sub-boreal spruce forest. *The Journal of Wildlife Management* **62**: 630–642.

Tsourgiannis L, Kazana V, Iakovoglou V. 2016. A comparative analysis of consumers' potential purchasing behaviour towards transgenic-derived forest products: the Greek case. In: Vettori C, Gallardo F, Häggman H, Kazana V, Migliacci F, Pilate G, Fladung M, eds. *Forestry sciences. Biosafety of forest transgenic trees*. Dordrecht, the Netherlands: Springer, 245–261.

Turner MG. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* **20**: 171–197.

Van der Plas F, Manning P, Soliveres S, Allan E, Scherer-Lorenzen M, Verheyen K, Wirth C, Zavala MA, Ampoorter E, Baeten L *et al.* 2016. Biotic homogenization can decrease landscape-scale forest multifunctionality. *Proceedings of the National Academy of Sciences, USA* **113**: 3557–3562.

Vander Wall SB. 1993. Cache site selection by chipmunks (*Tamias* spp.) and its influence on the effectiveness of seed dispersal in Jeffrey pine (*Pinus jeffreyi*). *Oecologia* **96**: 246–252.

Vander Wall SB. 1994. Removal of wind-dispersed pine seeds by ground-foraging vertebrates. *Oikos* **69**: 125.

Vander Wall SB. 1995. The effects of seed value on the caching behavior of yellow pine chipmunks. *Oikos* **74**: 533–537.

Vander Wall SB. 2000. The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). *Behavioral Ecology* **11**: 544–549.

Vander Wall SB. 2002. Masting in animal-dispersed pines facilitates seed dispersal. *Ecology* **83**: 3508–3516.

Vander Wall SB. 2003. Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. *Oikos* **100**: 25–34.

Vander Wall SB. 2008. On the relative contributions of wind vs. animals to seed dispersal of four Sierra Nevada pines. *Ecology* **89**: 1837–1849.

Vaske JJ, Beaman J, Barreto H, Shelby LB. 2010. An extension and further validation of the potential for conflict index. *Leisure Sciences* **32**: 240–254.

Verkaik I, Espelta JM. 2006. Post-fire regeneration thinning, cone production, serotiny and regeneration age in *Pinus halepensis*. *Forest Ecology and Management* **231**: 155–163.

Vettori C, Gallardo F, Häggman H, Kazana V, Migliacci F, Pilate G, Fladung M, eds. 2016. *Biosafety of forest transgenic trees*. Dordrecht, the Netherlands: Springer.

Vining KJ, Contreras RN, Ranik M, Strauss SH. 2012. Genetic methods for mitigating invasiveness of woody ornamental plants: research needs and opportunities. *HortScience* **47**: 1210–1216.

Walter C, Fladung M, Boerjan W. 2010. The 20-year environmental safety record of GM trees. *Nature Biotechnology* **28**: 656–658.

Wang ET, Sandberg R, Luo S, Khrebtukova I, Zhang L, Mayr C, Kingsmore SF, Schroth GP, Burge CB. 2008. Alternative isoform regulation in human tissue transcriptomes. *Nature* **456**: 470–476.

Ward C, Erdle T. 2015. Evaluation of forest management strategies based on Triad zoning. *The Forestry Chronicle* **91**: 40–51.

Waser NM, Chittka L, Price MV, Williams NM, Ollerton J. 1996. Generalization in pollination systems, and why it matters. *Ecology* **77**: 1043–1060.

Wenger K. 1954. The stimulation of loblolly pine seed trees by preharvest release. *Journal of Forestry* **52**: 115–118.

Westphal C, Steffan-Dewenter I, Tscharntke T. 2006. Bumblebees experience landscapes at different spatial scales: possible implications for coexistence. *Oecologia* **149**: 289–300.

Williams CG. 2009. *Conifer reproductive biology*. Dordrecht, the Netherlands: Springer.

Willson MF, Pendleton GW, Jones JD, Craig LF, Sherwin AE. 2012. Black bear (*Ursus americanus*) foraging on Black cottonwood (*Populus trichocarpa*) catkins in Southeast Alaska. *Northwestern Naturalist* **93**: 211–219.

Wisconsin Department of Natural Resources (WDNR). 2010. *Silviculture handbook*. [WWW document] URL http://dnr.wi.gov/topic/ForestManagement/documents/24315/32.pdf [accessed 23 December 2016].

Witmer MC. 2001. Nutritional interactions and fruit removal: cedar waxwing consumption of *Viburnum opulus* fruits in spring. *Ecology* **82**: 3120–3130.

Yang Y, Tang R-J, Jiang C-M, Li B, Kang T, Liu H, Zhao N, Ma X-J, Yang L, Chen S-L *et al.* 2015. Overexpression of the *PtSOS2* gene improves tolerance to salt stress in transgenic poplar plants. *Plant Biotechnology Journal* **13**: 962–973.

Yuccer C, Land SB, Kubiske M, Harkess R. 2003. Shoot morphogenesis associated with flowering in *Populus deltoides* (Salicaceae). *American Journal of Botany* **90**: 196–206.

Zasada JC, Sharik TL, Nygren M. 1992. *The reproductive process in boreal forest trees. A systems analysis of the global boreal forest*. Cambridge, UK: Cambridge University Press.

Zhang C, Norris-Caneda KH, Rottmann WH, Gulledge JE, Chang S, Kwan BY-H, Thomas AM, Mandel LC, Kothera TH, Victor AD *et al.* 2012. Control of pollen-mediated gene flow in transgenic trees. *Plant Physiology* **159**: 1319–1334.

Zhang B, Oakes AD, Newhouse AE, Baier KM, Maynard CA, Powell WA. 2013. A threshold level of oxalate oxidase transgene expression reduces *Cryphonectria parasitica*. *Transgenic Research* **22**: 973–982.

Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Notes S1 Literature search methods.

Notes S2 Guiding hypotheses.

Notes S3 Research suggestions.