NEWS AND VIEWS

PERSPECTIVE

Species integrity in trees

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From California sequoia, to Australian eucalyptus, to the outstanding diversity of Amazonian forests, trees are fundamental to many processes in ecology and evolution. Trees define the communities that they inhabit, are host to a multiplicity of other organisms and can determine the ecological dynamics of other plants and animals. Trees are also at the heart of major patterns of biodiversity such as the latitudinal gradient of species diversity and thus are important systems for studying the origin of new plant species. Although the role of trees in community assembly and ecological succession is partially understood, the origin of tree diversity remains largely opaque. For instance, the relative importance of differing habitats and phenologies as barriers to hybridization between closely related species is still largely uncharacterized in trees. Consequently, we know very little about the origin of trees species and their integrity. Similarly, studies on the interplay between speciation and tree community assembly are in their infancy and so are studies on how processes like forest maturation modifies the context in which reproductive isolation evolves. In this issue of Molecular Ecology, Lindtke et al. (2014) and Lagache et al. (2014) overcome some traditional difficulties in studying mating systems and sexual isolation in the iconic oaks and poplars, providing novel insights about the integrity of tree species and on how ecology leads to variation in selection on reproductive isolation over time and space.

Keywords: adaptation, community ecology, hybridization, speciation

Received 15 June 2014; revised 14 July 2014; accepted 17 July 2014

 […] from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved. Charles Darwin, 1859

Wherever we have a great array of allied sympatric species there must be an emphasis on very accurate

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Reproductive isolation, or the inability of individuals from different populations to reproduce as effectively as they do within their own population, is one of the bedrock concepts for understanding the origin of new species. Many traits reduce gene flow between populations by limiting the opportunity for interspecific mating (prezygotic isolation) or by reducing the fitness of hybrids (postzygotic isolation). As a consequence, populations retain their genetic and morphological integrity and continue along independent evolutionary trajectories. A common scenario where species integrity may dissolve occurs when two previously allopatric populations come into contact and hybridize. As populations mate and recombine their genomes, gene combinations that made them or that kept them different (e.g. coadapted gene complexes and genetic incompatibilities) may be lost and therefore lead to their fusion. In the past decade, several studies have explored the processes that prevent species from collapsing in the face of hybridization. However, most taxa examined are insects and a handful of other animals and plants. Studies of species integrity in trees are scarce, thus making Lindtke et al. (2014) and Lagache et al. (2014) studies timely for starting a broader examination of mechanisms of speciation.

There are several reasons why species integrity has been studied in selected organisms. Genetic studies, such as QTL mapping of adaptive and reproductive isolation traits, and quantification of reproductive isolation at different stages of species hybridization (e.g. fitness of F1 versus backcross hybrids) are amenable only in organisms with partial levels of reproductive isolation, short generation times, and of relatively small size. More difficult, the interplay between ecology and genetic factors leading to species integrity can be only studied in organisms where relevant crosses are possible and individuals can be grown under field conditions. Recent reviews on reproductive isolation barriers in plants found that prezygotic barriers play a larger role in species integrity than postzygotic barriers (Lowry et al. 2008). The argument is simple: because prezygotic barriers seem to be strong and they act early during the life cycle of plants, their net effect on total reproductive isolation is expected to be larger than subsequent postzygotic barriers. However, many prezygotic barriers, particularly those that depend on environmental conditions, could be reversible, or they could only evolve once there is strong postzygotic isolation in place (Coyne & Orr 2004; Seehausen et al. 2014). This has led to some students of speciation to argue that postzygotic barriers are
crucial, if not the most important to speciation (reviewed in Coyne & Orr 2004). Lindtke et al. (2014) and Lagache et al. (2014) contribute to this debate and shed light as to the processes that affect mating between tree species and between them and their hybrid offspring.

Lindtke et al. (2014) explored species integrity in a mosaic hybrid zone between *Populus alba* and *Populus tremula* in a floodplain forest in Italy where the distribution of the upland habitat species *P. tremula* overlaps with that of lowland *P. alba*. The two species—and their hybrids—can form vast mosaic hybrid zones in river valleys, where both parents and their hybrids can be found within metres of each other, thus minimizing the effects of habitat associations on mating probabilities. Previous observations (Lexer et al. 2010) had found that while hybrids were common, backcross genotypes were quite rare among adult trees, leading to the question of whether hybrids were mating with the parent species and producing viable offspring. In organisms suitable for glasshouse studies, controlled pollinations could have answered this question, but with large, long-lived trees, genetic sampling in the field offered an alternative approach. The authors genotyped by sequencing over 12,000 single nucleotide polymorphisms (SNPs) from adults and seeds produced by each species and as well as hybrid trees. Using a Bayesian admixture model, a large fraction of these data was used to estimate the proportion of matings within and between species, and between each parental species and their hybrid offspring. The model further enabled the study of mating patterns without the need to sample potential fathers by inferring the hybrid class of the pollen from genomic data of mothers and progeny. Estimates of parental and hybrid ancestry demonstrated that while backcross genotypes were rare in adults, they were more common among seeds (Fig. 1). The scarcity of backcross adults must stem from decreased fitness of those genotypes in the field, although whether this is dependent on the particular environment remains unclear. The authors hypothesized that the decreased fitness of backcross and late-generation hybrid individuals may be due to the breakdown of gene complexes. This study is important because it sheds light on the timing of reproductive isolation and suggests that postzygotic isolation can play a fundamental role in maintaining species integrity. However, the interaction of genetic and environmental factors involved in the persistence of these species still needs clarification, and thus it will be an important future direction in the system.

The second study (Lagache et al. 2014) examined genetic and ecological factors affecting hybridization in oaks. *Quercus petraea* exists within the range of *Quercus robur* in Europe. The two trees co-occur at many sites, but differ in their ecology. *Quercus robur* is an early-successional tree, while *Q. petraea* grows in mature forests, leading to differences in the relative densities of the two species at different locations.
sites. The dynamics of ecological succession lead to changes in the densities of the two hybridizing species over space and time, and heterospecific matings are expected to be more common when conspecifics are rare (Fig. 2). This rarity effect leads us to expect spatial heterogeneity in the probability of hybridization across the oak stand and at various stages of forest maturation. Paternity analysis of multiple offspring from each mother together with precise spatial data collected in the field allowed Lagache et al. (2014) to quantify the spatial and temporal effects of successions on rates of hybridization. Specifically, they were able to estimate the trees that sired each offspring from each mother together with precise spatial data collected in the field allowed Lagache et al. (2014) to quantify the spatial and temporal effects of successions on rates of hybridization. Specifically, they were able to estimate the trees that sired each offspring, and so the movement of pollen both within and into the studied plot. They then considered several factors that could potentially affect mating between any two trees—such as the date of flowering for those trees, differences in pollen production depending on tree size and differences in pollen dispersal depending on the elevation of the tree—and found that each of these factors significantly affected the probability of any two trees mating.

This study has several implications for our understanding of species integrity in trees. First, they found differences in hybridization probability between the two species. *Q. petraea* mothers were less likely to form hybrid offspring when pollinated with *Q. robur* pollen than the reciprocal cross. This suggests that there are asymmetric intrinsic barriers to hybridization. Intriguingly, *Q. petraea* is more likely to be swamped by *Q. robur* pollen as it moves into a *Q. robur* dominated stand. While Lagache et al. (2014) did not examine hybrid fitness in this study, other studies (e.g. Abadie et al. 2012) have found evidence for decreases. Hence, it is possible that these prezygotic barriers to hybridization have evolved in *Q. petraea* due to selection against hybrids. In fact, barriers to hybridization are not constant across individuals or across time. Early in succession, *Q. robur* trees may have little exposure to *Q. petraea* pollen. As succession proceeds, initial *Q. petraea* trees will likely face pollen limitation and a higher proportion of *Q. robur* pollen. Late in succession, the situation may be reversed, with increasingly dominant *Q. petraea* trees receiving conspecific pollen, but *Q. robur* trees now receiving higher levels of heterospecific pollen. Ecological dynamics will therefore alter hybridization probabilities, the strength of boundaries between species and the strength of selection favouring the evolution of prezygotic barriers. As with many ecological studies, the particular parameters estimated may differ from 1 year to the next and from place to place (e.g. Gerber et al. 2014). However, Lagache et al. (2014) have demonstrated that variation in reproductive barriers can be estimated in the field and need not be confined to qualitative arguments.

Many gaps persist in our knowledge of species integrity in trees. These and other recent studies (e.g. Foster et al. 2007; Roe et al. 2014) demonstrate that through the combination of modern genotypic techniques and sophisticated probabilistic models, we can dissect the ecology and genetics of reproductive isolation in these challenging study systems. Lamentably, lack of knowledge is not restricted to the origin and persistence of new tree species, but to many other organisms where ecological context may be relevant for the evolution of reproductive isolation between populations and where traditional genetic studies are unfeasible. Exploring the ecological context of species identity in trees and other little-studied taxonomic groups promises to shed light on the origin and maintenance of biodiversity.

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References


D.O.-B. and E.I.B. wrote together this article.

doi: 10.1111/mec.12867