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Biological relevance of polyploidy: ecology to genomics
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Plant polyploidy and the evolutionary ecology of plant/animal interactions

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Until recently almost nothing was known about the effects of plant polyploidy on interactions with herbivores and pollinators. Studies of the saxifrage *Heuchera grossulariifolia* throughout its geographical range in the US northern Rockies have shown that autopolyploidy has probably arisen multiple times within this species since the end of the Pleistocene. Tetraploids from those different origins experience higher levels of attack by the moth *Greya politella* (Prodoxidae) than sympatric or parapatric diploids. In addition, within one intensively studied region, the plants are also attacked by two other lepidopteran species: *G. piperella*, which preferentially attack diploids, and *Eupithecia misturata* (Geometridae), which preferentially attacks tetraploids. Sympatric diploid and tetraploid plants also differ in the overall suites of pollinators they attract. Hence, the evolution of polyploid populations has the potential to change significantly the evolutionary ecology of interactions with herbivores and pollinators. Because a large number of plant lineages include polyploid species, the evolution of plant polyploidy may have had major effects on the interaction structure of terrestrial communities. © 2004 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2004, **82**, 511–519.

ADDITIONAL KEYWORDS: autopolyploidy – *Eupithecia misturata* – *Greya piperella* – *Greya politella* – *Heuchera grossulariifolia* – plants – pollination – repeated origins.

INTRODUCTION

Despite the commonness of polyploidy among plant taxa (Grant, 1981; Masterson, 1994), we have until recently known almost nothing about the ways in which polyploidy has shaped the evolution and ecology of interactions with animals. Somehow, polyploidy has simply remained outside the theoretical and empirical framework that has blossomed in recent years in our understanding of the evolutionary ecology and genetics of plant/animal interactions. Part of the problem is that some of the needed population genetic theory of polyploidy has developed only within the past decade (Bever & Felber, 1992; Felber & Bever, 1997; Kirkpatrick, Johnson & Barton, 2002; Wu, Ma & Casella, 2002; Husband, 2004 – this issue). Another part of the problem is that only with the development of flow cytometry as a tool for assessing DNA content and ploidy (Galbraith *et al*., 1983; de Laat, Gohde & Vogelzang, 1987; Arumuganathan & Earle, 1991) has it become practical to evaluate hundreds of individuals and determine large-scale patterns in the geographical distribution of polyploidy.

With those technical hurdles partially overcome, ecological and evolutionary studies of plant polyploidy

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across natural environments have begun to flourish. Most of these studies are on the origins of polyploidy (e.g. Ramsey & Schemske, 1998, 2002; Ainouche, Baumel & Salmon, 2004 – this issue), breeding systems (e.g. Cook & Soltis, 1999; Husband *et al*., 2002; Pannell, Obbard & Buggs, 2004 – this issue) or the effects of polyploidy on traits, physiological ecology and geographical distribution of polyploids (e.g. Lumaret *et al*., 1997; Husband & Schemske, 1998; Husband, 2000; Trewick *et al*., 2002; Brochmann *et al*., 2004 – this issue). In some instances, there are studies of plant/animal interactions in polyploid species, but without directly comparable studies of diploid populations or sister species that could provide a basis for comparison (Simon *et al*., 2001). The few studies that have undertaken comparative evaluations of attack on diploids and polyploids by herbivores (Thompson *et al*., 1997; Nuismer & Thompson, 2001) or pollinators (Segraves & Thompson, 1999; Husband, 2000) have shown strong differentiation in the use of plants with different ploidal levels.

There are three reasons why studies of plant polyploidy must be expanded to include comparative analyses of the evolutionary ecology of plant/animal interactions in diploid and polyploid species. First, as the distribution of polyploidy among plants has been evaluated across genera and families, it has become clear that many taxa contain polyploids. In fact, many plant taxa that have been studied intensively by ecologists and evolutionary biologists working on plant/animal interactions contain polyploid lineages. Examples include families such as the Asteraceae, Brassicaceae, Poaceae and Saxifragaceae, and genera such as *Arabidopsis*, *Artemisia* and *Mimulus*. Second, we now know that polyploidy may arise repeatedly within plant lineages, indicating that polyploid formation is a highly dynamic process (Soltis & Soltis, 1995, 1999 and Abbott & Lowe, 2004; Soltis *et al*., 2004 – both this issue). If polyploidy affects plant/animal interactions, then repeated evolution of polyploid lineages could create highly dynamic geographical patterns in the ecology and evolution of interspecific interactions. Third, many important forage and crop plants are polyploid, including alfalfa, wheat, oats, coffee, potatoes, sugar cane, cotton, peanuts, bananas, tobacco and strawberries. Consequently, studies of naturally occurring polyploids and their interactions with other taxa could be invaluable as aids in the conservation of many plant lineages, breeding for durable resistance against pests, and increased pollination in crop plants.

Here we evaluate what we currently know and need to know about the ways in which plant polyploidy affects interactions with herbivores and pollinators within natural populations. The data are sparse and only one species, the saxifrage *Heuchera grossulariifolia*, has been studied in sufficient detail to allow assessment of the overall effects of polyploidy on interactions with herbivores and pollinators. We therefore first review what is known for that species, and then pose several critical questions that address gaps in our current understanding of how polyploidy shapes the evolution of interspecific interactions and the organization of terrestrial biodiversity.

POLYPLOIDY AND HERBIVORY IN *HEUCHERA GROSSULARIIFOLIA*

As is often the case in science, serendipity played a major role in the development of *Heuchera grossulariifolia* as a model system for analysis of how plant polyploidy shapes plant/animal interactions. During studies of the interaction between the moth *Greya politella* and the widespread saxifrage *Lithophragma parviflorum* in north-western USA (Thompson & Pellmyr, 1992; Pellmyr & Thompson, 1996), some populations of the moths were found on an endemic and closely related saxifrage, *H. grossulariifolia* in northern Idaho, USA. *Greya* moths tend to be highly host specific within local populations. Use of the endemic *H. grossulariifolia* in these northern populations therefore provided an opportunity to evaluate post-Pleistocene patterns of geographical divergence in an insect/plant interaction as it diversified in a previously glaciated region.

Greya moths are close relatives of yucca moths, but they are specialists either on plants in the Saxifragaceae or Apiaceae rather than the Agavaceae. Some *Greya* moths, including *G. politella*, are pollinating seed parasites, pollinating their host plants while laying eggs in their flowers (Davis, Pellmyr & Thompson, 1992; Pellmyr & Thompson, 1992, 1996; Thompson & Pellmyr, 1992; Thompson & Cunningham, 2002). Unlike yucca moths, pollination is passive rather than active during oviposition. Study of the pattern of floral visitation and herbivory by this moth on *H. grossulariifolia* soon made it evident that use of this plant as a host by *G. politella* was highly patchy, occurring at high levels in parts of some river systems but not in others. Serendipitously, Wolf, Soltis & Soltis (1989, 1990) discovered at about the same time that some *H. grossulariifolia* populations were autotetraploid whereas others were diploid. The juxtaposition of the field observations on the interactions with the moths and the discovery of polyploidy in this plant species set the stage for a series of still-continuing studies on how polyploidy affects herbivory and pollination across complex geographical landscapes.

Heuchera grossulariifolia is endemic to the US northern Rockies, ranging from the mountains of central Idaho into western Montana. It is restricted primarily to basaltic and granitic rock faces and talus

slopes along rivers, making the distributional limits of most populations relatively easy to assess. This endemism and restricted habitat distribution have made it possible to assess the geographical distribution of polyploidy throughout the geographical range of the species. Initial surveys showed at least three geographically separated regions with polyploid populations. Within each of those regions diploid and tetraploid populations occurred either sympatrically or parapatrically over short geographical distances (Fig. 1).

The most parsimonious explanation for the patchy occurrence of these polyploid populations is that they have arisen repeatedly in the US northern Rockies since glacial retreat at the end of the Pleistocene. Phylogeographical studies using sequence variation in chloroplast DNA and restriction site polymorphisms (RFLPs) indicated that autopolyploidy has arisen at least twice, and potentially up to seven times, during the evolutionary history of this species (Segraves *et al*., 1999) and subsequent work using other molecular markers has corroborated that result (J. N. Thompson, unpubl. data). The pattern, however, is geographically complex. Some local polyploid populations do not seem to have arisen directly from neighbouring diploid populations, and additional detailed sampling throughout the geographical range is beginning to resolve the phylogeography of polyploidy more fully.

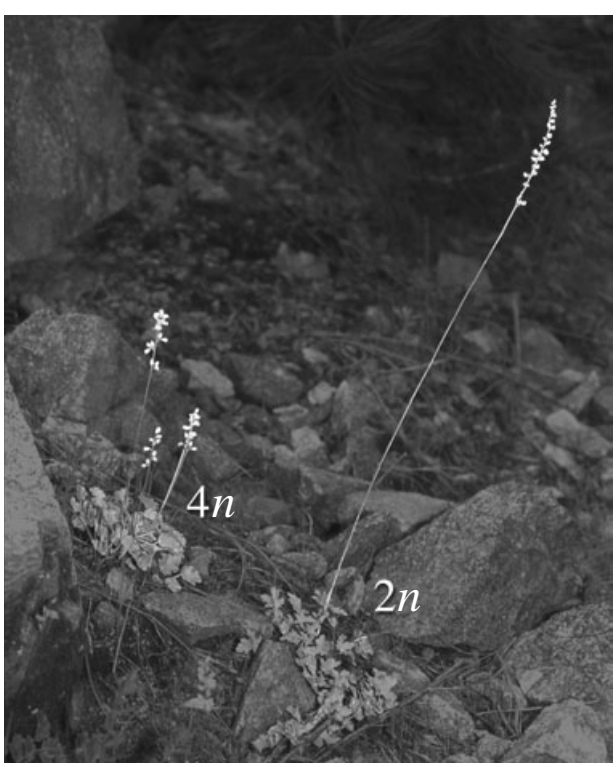

Figure 1. Diploid (2*n*) and tetraploid (4*n*) *Heuchera grossulariifolia* growing sympatrically along the Salmon River, Idaho, USA.

Greya politella females lay their eggs into the flowers of *H. grossulariifolia*. Systematic collection and dissection of floral capsules throughout the range of this species showed that both diploid and tetraploid populations are attacked (Fig. 2). Wherever diploid and tetraploid populations are sympatric or parapatric, however, the moths attack a higher percentage of tetraploid capsules (Fig. 3). Because the phylogeographical analyses of *H. grossulariifolia* suggest that at least two, and perhaps all three, of the regions in this analysis represent separate origins of polyploidy, higher attack on tetraploids is not simply a consequence of a particular polyploid genotype.

Subsequent work has confirmed that result. *Greya politella* attack on pairs of diploid and tetraploid plants distributed across a zone of sympatry along the Salmon River in Idaho has consistently been higher on tetraploid than on diploid plants (Nuismer & Thompson, 2001) (Fig. 4). In addition, the mean number of larvae per attacked plant is higher on tetraploids than on diploids.

Greya politella preference for tetraploid plants appears to have evolved after colonization of *Heuchera*, at least in populations along the Salmon River. The river runs generally east to west through this part of Idaho, and flowering times of plants in the deep river canyon can differ by more than 3 weeks on opposite sides of the river. The dry south-facing slopes on the north side of the river harbour extensive populations of *Lithophragma parviflorum*, the more common host for *G. politella* in the Pacific Northwest. These moth populations are generally allochronically isolated from the moths feeding on *Heuchera* along the moister north-facing slopes on the south side of the river. When diploid and tetraploid *Heuchera* were experimentally distributed throughout the *Lithophragma* population on the north side of the river, the *Lithophragma*-adapted moths did not distinguish between diploid and tetraploid plants (Janz & Thompson, 2002). Similarly, no-choice and choice preference experiments showed that these *Lithophragma*-adapted moths exhibit no preference for either diploid or tetraploid *H. grossulariifolia*. Moreover, the field experiments and the preference experiments showed that these moths exhibit very little tendency at all to lay eggs in *Heuchera* (Janz & Thompson, 2002).

Hence, populations of the moths on *Lithophragma* and *Heuchera* may be host races, and preference for tetraploids in the *Heuchera* host race may have evolved since the end of the Pleistocene, when the populations expanded into these habitats. These tentative conclusions require corroboration through mating

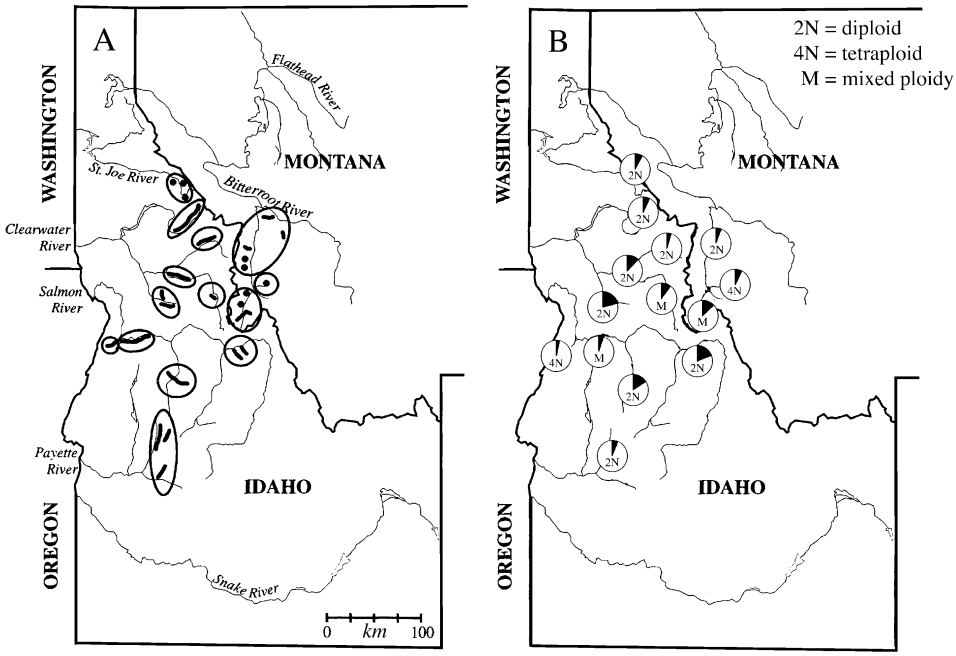

Figure 2. A, Distribution of sampling sites for polyploidy in *Heuchera grossulariifolia* among river systems in the US northern Rockies, and B, the percentage of floral capsules containing larvae (black sections of pie diagrams) within those sampled river systems. Modified from Thompson *et al*. (1997).

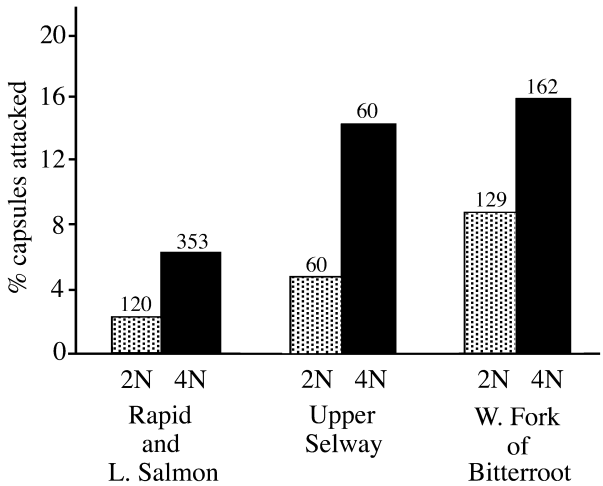

Figure 3. The proportion of diploid and tetraploid *Heuchera grossulariifolia* floral capsules attacked by the moth *Greya politella* in three river systems in the US northern Rockies: Rapid River and Lower Salmon River, Idaho; Selway River, Idaho; West Fork of the Bitterroot River, Montana. Numbers above bars are the number of capsules dissected from each population. Attack on tetraploids is significantly greater than attack on diploids in these populations, based upon nominal logistic regression. Modified from Thompson *et al*. (1997).

experiments between moths on the different host species. Because oviposition preference in at least some Lepidoptera is governed primarily by one or more genes on the X chromosome (Thompson, 1988; Janz, 1998), studies comparing parental preference with that of F_1 hybrids may give considerable information on whether the moths are in fact host races. These studies would help determine the extent to which the differences in host use are genetically based.

Tetraploidy in *Heuchera* has non-uniform effects on herbivores (Nuismer & Thompson, 2001). The Salmon River population of *H. grossulariifolia* is attacked not only by *G. politella* but also by two other lepidopteran species. *Greya piperella* is a stem borer, and it attacks diploid plants more commonly than tetraploid plants (Fig. 5). *Eupithecia misturata* is a geometrid moth that lays a batch of eggs on the floral stalk. The larvae feed externally both on flowers and the floral stalk. Female *E. misturata* oviposit significantly more eggs on to tetraploid plants than onto diploid plants. Together these three lepidopteran species are the major herbivores of *H. grossulariifolia*. (A noctuid species that grazes among plants is an occasional herbivore, but its preferences have not yet been quantified.) Whether diploids or tetraploids would be favoured by natural selection in any local habitat must therefore depend in part upon the relative abundances of these three moth species.

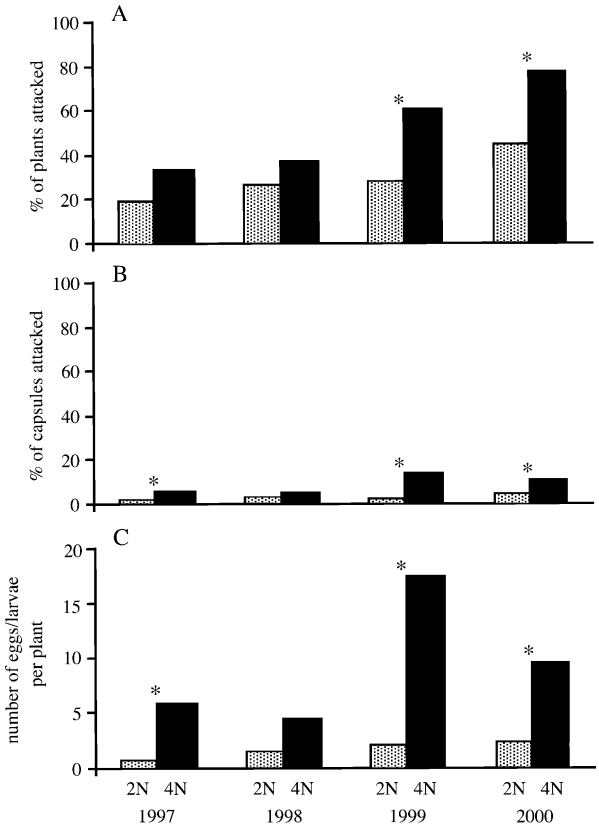

Figure 4. The percentage of sympatric diploid and tetraploid *Heuchera grossulariifolia* plants (A) and capsules (B) attacked by the moth *Greya politella* along the Salmon River, Idaho, USA, and the number of eggs laid per plant (C) during four years of study. Modified from Nuismer & Thompson (2001).

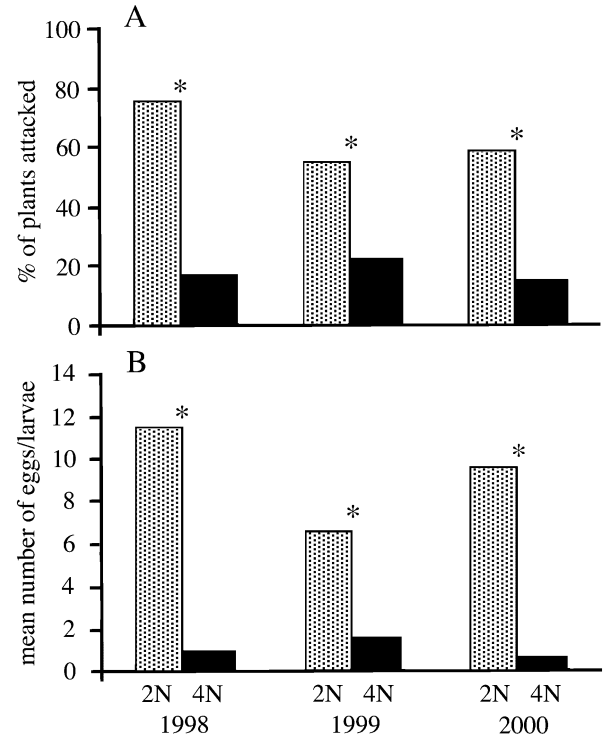

Figure 5. The percentage of sympatric diploid and tetraploid *Heuchera grossulariifolia* plants attacked by the moth *Greya piperella* along the Salmon River, Idaho, USA (A), and the number of eggs laid per plant (B) during three years of study. Modified from Nuismer & Thompson (2001).

POLYPLOIDY AND POLLINATION IN *H. GROSSULARIIFOLIA*

Polyploidy in *H. grossulariifolia* also has major effects on visitation by pollinators. *Greya politella* is among the potential pollinators. While ovipositing, *G. politella* females passively pollinate the flowers as pollen adhering to the abdomen from visits to previous flowers rubs off on to the stigma. These moths are close relatives of yucca moths (Brown *et al.*, 1994; Pellmyr *et al.*, 1996; Pellmyr & Leebens-Mack, 1999) and, like the yucca moths, are major pollinators of some plants they use as hosts (Thompson & Pellmyr, 1992; Pellmyr *et al.*, 1996; Thompson & Cunningham, 2002). *Heuchera grossulariifolia*, however, is also visited by at least 25 other insect species across its geographical range (K. Merg & J. N. Thompson, unpubl. data). Along the Salmon River, at least 15 insect species or species complexes visit the flowers (Segraves & Thompson, 1999).

A 1-year study of diploid and tetraploid pairs separated by less than 1 m showed that the majority of visits are by bees, but the proportion of visits to plants of each ploidy differs greatly among bee species (Segraves & Thompson, 1999). For example, *Lasioglossum* bees constituted about one-quarter of the visits to diploids but only one-tenth of the visits to tetraploids. Even more interestingly, *Bombus centralis* queens visited tetraploids more frequently whereas workers visited diploids more frequently. The moth *G. politella* visited tetraploid flowers five times more frequently than diploid flowers. The only other non-bee species that was a common visitor was the bee-fly *Bombyllius major*, which visited tetraploid flowers six times more frequently than diploid flowers. These differences were evident in the mean number of visits to diploid and tetraploid flowers during 30-min observation periods (Table 1). Some other species showed no difference in visitation to diploids and tetraploids, but the sample sizes were low for most of these species.

POLYPLOIDY AND ITS OVERALL EFFECTS ON INTERSPECIFIC INTERACTIONS IN *H. GROSSULARIIFOLIA*

The results for herbivory and pollination together indicate that the evolution of polyploidy has had pro-

Table 1. Visits to pairs of diploid and tetraploid flowers of *Heuchera grossulariifolia* by representative major floral visitors. Values are the mean number of visits (±SE, *N* in parentheses) during each 30-min observation period. Differences were evaluated using univariate analysis of variance. Condensed from Segraves & Thompson (1999)

Insect visitor	Diploid mean	Tetraploid mean	*F*	*P*
Bees				
Lasioglossum spp.	1.7 ± 0.19 (52)	0.7 ± 0.22 (19)	11.59	0.001
Bombus centralis				
Queens	0.4 ± 0.11 (14)	1.4 ± 0.17 (44)	18.44	0.0001
Workers	1.2 ± 0.25 (12)	0.1 ± 0.10 (1)	–	
Flies				
Bombyllius major	0.3 ± 0.11 (7)	1.7 ± 0.26 (45)	31.95	0.0001
Moths				
Greya politella	0.3 ± 0.12 (4)	1.3 ± 0.31 (20)	8.16	0.009

found effects on the network of interactions between *H. grossulariifolia* and the insects with which it interacts. Along the Salmon River, diploids and tetraploids differ sufficiently in morphology to be distinguished easily by the human eye. In other river systems within northern Idaho, however, it is not possible to discern any consistent morphological difference that would allow ready identification in the field. Nonetheless, studies now reaching completion indicate that insects differentiate among ploidy in these regions as well (K. Merg & J. N. Thompson, unpubl. data). Those results have highlighted how easy it would be to miss polyploidy as a potentially important factor shaping interactions between plants and insects. 'Mean' pattern of herbivore attack or floral visitation within a sympatric population or parapatric region of diploids and tetraploids would be a meaningless result, unless the results were partitioned by ploidy. Given the prevalence of plant polyploidy, the potential for such obfuscation may be common in studies of plant/insect interactions within some plant families.

Whether diploid and tetraploid *H. grossulariifolia* constitute one species or a complex of species is not yet known. The potential for cross-pollination between diploids and tetraploids certainly still exists. Although floral visitors differ in their preference for the diploids or polyploids, no major visitor is restricted to plants of one or the other ploidy. Moreover, it is not yet clear whether genetic incompatibility between diploids and tetraploids is complete. Initial crossing experiments indicated little potential for successful interbreeding between diploids and tetraploids (Wolf *et al.*, 1989, 1990), but subsequent studies have suggested some potential for successful introgression of genes (K. Merg & J. N. Thompson, unpubl. data; C. Fernandez & J. N. Thompson, unpubl. data).

Overall, it appears that polyploidy has created a dynamic evolutionary environment for the diversification of populations of *H. grossulariifolia* and its interactions with insects throughout its geographical range. Polyploidy changes the selective environment imposed both by herbivores and pollinators. Moreover, repeated polyploid events in different parts of the geographical range create opportunities for complex patterns of geographical differentiation in interspecific interactions and the origins of new species.

MAJOR QUESTIONS ON POLYPLOIDY AND PLANT/ANIMAL INTERACTIONS

The results for *Heuchera* and its herbivores and pollinators, together with related ecological studies on polyploidy in other plants, motivate a set of questions for future research.

Are herbivore (and pathogen) lineages generally more likely or less likely to colonize polyploid than diploid plant lineages?

Most host shifts in insects are onto plant species that are closely related to their ancestral hosts, but some shifts are onto distantly related plants within the same family or onto different families. Many such shifts are explicable by the distribution of chemical compounds within and among plant families, but it would be useful to know how polyploidy affects the probability of host shifts. Assessing such probabilities has become an increasingly important part of developing methods for reconstructing the phylogenetic history of co-diversification in interacting taxa (Charleston & Perkins, 2003; Huelsenbeck, Rannala & Larget, 2003).

Does polyploidy in plants have predictable effects on the evolution of pollinator/plant interactions?

It is currently unknown whether polyploidy usually creates instantaneous assortative mating by restricting movement of pollinators between diploids and

tetraploids. In one of the few studies of natural populations of diploid and tetraploid plants other than *H. grossulariifolia*, Husband (2000) found that bumblebees, honeybees, and leaf-cutter bees all visited diploid more than tetraploid *Chamerion angustifolium*, but these insects moved between plants differing in ploidy. The results for *H. grossulariifolia* also show that pollinators have not been wholly excluded from either diploids or tetraploids. Instead, the frequencies of visits to the two cytotypes are different, and the overall pattern seems to hold for separate origins of polyploidy in different river systems (K. Merg & J. N. Thompson, unpubl. data). That result, of course, is for a single species that has diversified only in the past 10 000 years.

If polyploidy has predictable effects on breeding systems, then it could impose predictable effects on suites of floral adaptation. Citing evidence from the Solanaceae, Miller & Venable (2000) proposed that polyploidy may facilitate the evolution of gender dimorphism. If such a dramatic shift in breeding system results from polyploidy, then a whole range of more subtle changes affecting pollinator/plant interactions could be common. Other potential effects of polyploidy, such as increased self-compatibility, could also contribute to predictable changes in floral adaptation.

How does plant polyploidy shape the geographical mosaic of coevolution?

Recent mathematical models of coevolution in haploid and diploid species have suggested that ploidy can alter the rate and amplitude of coevolutionary dynamics (Switkes & Moody, 2001). If polyploidy does, in fact, have major effects on the local dynamics of coevolution and patterns of gene flow among populations, then it may shape the overall geographical structure and dynamics of coevolution. The past decade of studies has shown that coevolution often may be a highly dynamic geographical process. Natural selection on interactions differs among environments, resulting in regions where coevolutionary selection is strong, called coevolutionary hotspots, or absent, called coevolutionary coldspots (Benkman, Holimon & Smith, 2001; Brodie, Ridenhour & Brodie, 2002; Parchman & Benkman, 2002; Thompson & Cunningham, 2002). Continued gene flow among populations may maintain the genetic diversity for the coevolutionary process at the metapopulation scale or broader geographical scales (Burdon, Thrall & Lawrence, 2002). The geographical mosaic theory of coevolution predicts that this combination of selection mosaics, coevolutionary hotspots, and trait remixing will create an almost inevitable geographical mosaic of coevolved traits in interacting species, few of which will ever become fixed traits of coevolving species (Thompson, 1994, 1999). Moreover, this coevolutionary process will generate a mosaic or cline of adaptation and maladaptation across complex landscapes (Nuismer, Thompson & Gomuljiewicz, 1999, 2003; Gomulkiewicz *et al.*, 2000). Repeated evolution of polyploidy within plant species could contribute to creating the mosaic. Where polyploidy creates new species, it would increase the geographical discontinuities among coevolving populations. Where diploids and polyploids are not fully incompatible, it would fuel the selection mosaic by altering the structure and outcome of local interactions with herbivores and pollinators.

How much of terrestrial diversity is the result of plant polyploidy and its effects on the diversification of plant/animal interactions?

If, in fact, most plant species are polyploid, and if polyploidy commonly reshapes plant/animal interactions, then it may have been a major force in the organization of terrestrial diversity. How would the structure of terrestrial communities have looked if plant polyploidy had not been a major part of plant diversification? There is no simple way to answer this question. Nonetheless, insights will be possible in coming years through several kinds of study. The most direct are more studies like those on *H. grossulariifolia*, evaluating local and geographical diversification of particular plant/animal interactions as mediated by polyploidy. These studies will show how phylogenetic lineages may diversify through the evolution of polyploid populations, especially in lineages where polyploidy has arisen multiple times. In addition, analyses of diversification within plant lineages whose herbivores and pollinators are well known will allow broader analyses of patterns of co-diversification and host shifts in animals using diploid and polyploid plant species. Also, comparative biogeographical analyses of floras differing in the frequency of polyploids should help in analyses of how plant polyploidy affects the development of biological communities more generally. Finally, studies of neopolyploids will help sort out which effects of polyploidy are instantaneous byproducts of polyploid formation and which effects evolve later either as a direct or indirect response to polyploidy (Ramsey & Schemske, 1998, 2002).

CONCLUSIONS

Polyploidy is such a common component of plant evolution that it must be part of any general theory of the evolutionary ecology and genetics of plant/animal interactions. The few studies available suggest that

polyploidy influences herbivores and pollinators, and its effects can differ among even closely related herbivore species. Polyploidy is therefore likely to have important influences on the structure and diversification of terrestrial communities.

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REFERENCES

Abbott RJ, Lowe AJ. 2004. Origins, establishment and evolution of new polyploid species: *Senecio cambrensis* and *S. eboracensis* in the British Isles. *Biological Journal of the Linnean Society* **82:** 467–474.

Ainouche ML, Baumel A, Salmon A. 2004. *Spartina anglica* C. E. Hubbard: a natural model system for studying early evolutionary changes that affect allopolyploid genomes. *Biological Journal of the Linnean Society* **82:** 475–484.

Arumuganathan K, Earle ED. 1991. Estimation of nuclear DNA content of plants by flow cytometry. *Plant Molecular Biology Reporter* **9:** 229–233.

Benkman CW, Holimon WC, Smith JW. 2001. The influence of a competitor on the geographic mosaic of coevolution between crossbills and lodgepole pine. *Evolution* **55:** 282–294.

Bever JD, Felber F. 1992. The theoretical population genetics of autopolyploidy. *Oxford Surveys in Evolutionary Biology* **8:** 185–217.

Brochmann C, Brysting AK, Alsos IG, Borgen L, Grundt HH, Scheen A-C, Elven R. 2004. Polyploidy in arctic plants. *Biological Journal of the Linnean Society* **82:** 521–536.

Brodie ED Jr, Ridenhour BJ, Brodie ED III. 2002. The evolutionary response of predators to dangerous prey: hotspots and coldspots in the geographic mosaic of coevolution between newts and snakes. *Evolution* **56:** 2067–2082.

Brown JM, Pellmyr O, Thompson JN, Harrison RG. 1994. Mitochondrial DNA phylogeny of the Prodoxidae (Lepidoptera: Incurvarioidea) indicates rapid ecological diversification of yucca moths. *Annals of the Entomological Society of America* **87:** 795–802.

Burdon JJ, Thrall PH, Lawrence GJ. 2002. Coevolutionary patterns in the *Linum marginale – Melampsora lini* association at a continental scale. *Canadian Journal of Botany* **80:** 288–296.

Charleston MA, Perkins SL. 2003. Lizards, malaria, and jungles in the Caribbean. In: Page RDM, ed. *Tangled trees: phylogeny, cospeciation, and coevolution*. Chicago: University of Chicago, 65–92.

Cook LM, Soltis PS. 1999. Mating systems of diploid and allotetraploid populations of *Tragopogon* (Asteraceae) I. Natural populations. *Heredity* **82:** 237–244.

Davis DR, Pellmyr O, Thompson JN. 1992. Biology and systematics of *Greya* Busck and *Tetragma*, new genus (Lepidoptera: Prodoxidae). *Smithsonian Contributions to Zoology* **524:** 1–88.

Felber F, Bever JD. 1997. Effect of triploid fitness on the coexistence of diploids and tetraploids. *Biological Journal of the Linnean Society* **60:** 95–106.

Galbraith DW, Harkins KR, Maddox JM, Ayres NM, Sharma DP, Firoozabady E. 1983. Rapid flow cytometric analysis of the cell cycle in intact plant tissues. *Science* **220:** 1049–1051.

Gomulkiewicz R, Thompson JN, Holt RD, Nuismer SL, Hochberg ME. 2000. Hot spots, cold spots, and the geographic mosaic theory of coevolution. *American Naturalist* **156:** 156–174.

Grant V. 1981. *Plant speciation*. New York: Columbia University Press.

Huelsenbeck JP, Rannala B, Larget B. 2003. A statistical perspective for reconstructing the history of host–parasite associations. In: Page RDM, ed. *Tangled trees: phylogeny, cospeciation, and coevolution*. Chicago: University of Chicago, 93–119.

Husband BC. 2000. Constraints on polyploid evolution: a test of the minority cytotype exclusion principle. *Proceedings of the Royal Society of London B* **267:** 217–223.

Husband BC. 2004. The role of triploid hybrids in the evolutionary dynamics of mixed-ploidy populations. *Biological Journal of the Linnean Society* **82:** 537–546.

Husband BC, Schemske DW, Burton TL, Goodwillie C. 2002. Pollen competition as a unilateral reproductive barrier between sympatric diploid and tetraploid *Chamerion angustifolium*. *Proceedings of the Royal Society of London B* **269:** 2565–2571.

Husband BC, Schemske DW. 1998. Cytotype distribution at a diploid–tetraploid contact zone in *Chamerion (Epilobium) angustifolium* (Onagraceae). *American Journal of Botany* **85:** 1688–1694.

Janz N. 1998. Sex-linked inheritance of host-plant specialization in a polyphagous butterfly. *Proceedings of the Royal Society of London B* **265:** 1675–1678.

Janz N, Thompson JN. 2002. Plant polyploidy and host expansion in an insect herbivore. *Oecologia* **130:** 570–575.

Kirkpatrick M, Johnson T, Barton N. 2002. General models of multilocus evolution. *Genetics* **161:** 1727–1750.

de Laat AMM, Göhde W, Vogelzang MJDC. 1987. Determination of ploidy of single plants and plant populations by flow cytometry. *Plant Breeding* **99:** 303–307.

Lumaret R, Guillerm J-L, Maillet J, Verlaque R. 1997. Plant species diversity and polyploidy in islands of natural vegetation isolated in extensive cultivated lands. *Biodiversity and Conservation* **6:** 591–613.

Masterson J. 1994. Stomatal size in fossil plants – evidence for polyploidy in majority of angiosperms. *Science* **264:** 421–424.

Miller JS, Venable DL. 2000. Polyploidy and the evolution of gender dimorphism in plants. *Science* **289:** 2335–2338.

Nuismer SL, Thompson JN. 2001. Plant polyploidy and non-uniform effects on insect herbivores. *Proceedings of the Royal Society of London B* **268:** 1937–1940.

Nuismer SL, Thompson JN, Gomulkiewicz R. 1999. Gene flow and geographically structured coevolution. *Proceedings of the Royal Society of London B* **266:** 605–609.

Nuismer SL, Thompson JN, Gomulkiewicz R. 2003. Coevolution between hosts and parasites with partially overlapping geographic ranges. *Journal of Evolutionary Biology* **16:** 1337–1345.

Pannell JR, Obbard DJ, Buggs RA. 2004. Polyploidy and the sexual system: what can we learn from *Mercurialis annua*? *Biological Journal of the Linnean Society* **82:** 547–560.

Parchman TL, Benkman CW. 2002. Diversifying coevolution between crossbills and black spruce on Newfoundland. *Evolution* **56:** 1663–1672.

Pellmyr O, Leebens-Mack J. 1999. Forty million years of mutualism: evidence for Eocene origin of the yucca–yucca moth association. *Proceedings of the National Academy of Sciences, USA* **96:** 9178–9183.

Pellmyr O, Thompson JN. 1992. Multiple occurrences of mutualism in the yucca moth lineage. *Proceedings of the National Academy of Sciences, USA* **89:** 2927–2929.

Pellmyr O, Thompson JN. 1996. Sources of variation in pollinator contribution within a guild: the effects of plant and pollinator factors. *Oecologia* **107:** 595–604.

Pellmyr O, Thompson JN, Brown JM, Harrison RG. 1996. Evolution of pollination and mutualism in the yucca moth lineage. *American Naturalist* **148:** 827–847.

Ramsey J, Schemske DW. 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics* **29:** 467–501.

Ramsey J, Schemske DW. 2002. Neopolyploidy in flowering plants. *Annual Review of Ecology and Systematics* **33:** 589–639.

Segraves KA, Thompson JN. 1999. Plant polyploidy and pollination: floral traits and insect visits to diploid and tetraploid *Heuchera grossulariifolia*. *Evolution* **53:** 1114–1127.

Segraves KA, Thompson JN, Soltis PS, Soltis DE. 1999. Multiple origins of polyploidy and the geographic structure of *Heuchera grossulariifolia*. *Molecular Ecology* **8:** 253–262.

Simon J, Bosch M, Molero J, Blanche C. 2001. Conservation biology of the Pyrenean larkspur (*Delphinium montanum*): a case of conflict of plant versus animal conservation? *Biological Conservation* **98:** 305–314.

Soltis DE, Soltis PS. 1995. The dynamic nature of polyploid genomes. *Proceedings of the National Academy of Sciences, USA* **92:** 8089–8091.

Soltis DE, Soltis PS. 1999. Polyploidy: recurrent formation and genome evolution. *Trends in Ecology and Evolution* **14:** 348–352.

Soltis DE, Soltis PS, Pires JC, Kovarik A, Tate JA, Mavrodiev E. 2004. Recent and recurrent polyploidy in *Tragopogon* (Asteraceae): cytogenetic, genomic and genetic comparisons. *Biological Journal of the Linnean Society* **82:** 485–501.

Switkes JM, Moody ME. 2001. Coevolutionary interactions between a haploid species and a diploid species. *Journal of Mathematical Biology* **42:** 175–194.

Thompson JN. 1988. Variation in preference and specificity in monophagous and oligophagous swallowtail butterflies. *Evolution* **42:** 118–128.

Thompson JN. 1994. *The coevolutionary process*. Chicago: University of Chicago Press.

Thompson JN. 1999. Specific hypotheses on the geographic mosaic of coevolution. *American Naturalist* **153:** S1–S14.

Thompson JN, Cunningham BM. 2002. Geographic structure and dynamics of coevolutionary selection. *Nature* **417:** 735–738.

Thompson JN, Cunningham BM, Segraves KA, Althoff DM, Wagner D. 1997. Plant polyploidy and insect/plant interactions. *American Naturalist* **150:** 730–743.

Thompson JN, Pellmyr O. 1992. Mutualism with pollinating seed parasites amid co-pollinators: constraints on specialization. *Ecology* **73:** 1780–1791.

Trewick SA, Morgan-Richards M, Russell SJ, Henderson S, Rumsey FJ, Pinter I, Barrett JA, Gibby M, Vogel JC. 2002. Polyploidy, phylogeography and Pleistocene refugia of the rockfern *Asplenium ceterach*: evidence from chloroplast DNA. *Molecular Ecology* **11:** 2003–2012.

Wolf PG, Soltis DE, Soltis PS. 1990. Chloroplast-DNA and allozymic variation in diploid and autotetraploid *Heuchera grossularifolia* (Saxifragaceae). *American Journal of Botany* **77:** 232–244.

Wolf PG, Soltis PS, Soltis DE. 1989. Tetrasomic inheritance and chromosome pairing behaviour in the naturally occurring autotetraploid *Heuchera grossulariifolia* (Saxifragaceae). *Genome* **32:** 655–659.

Wu R, Ma C-X, Casella G. 2002. A bivalent polyploid model for linkage analysis in outcrossing tetraploids. *Theoretical Population Biology* **62:** 129–151.