Ploidy influences rarity and invasiveness in plants

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Summary

1. The factors associated with plant species’ endangerment and (conversely) invasiveness are of broad interest due to their potential value in explaining the causes and consequences of population status. While most past work has focussed on ecological variables, recent work suggests that genetic attributes may be strongly associated with plant species status.

2. We collated data on chromosome numbers for 640 endangered species (worldwide) and their 9005 congeners, and for 81 invasive species and their 2356 congeners. We related ploidy (diploid versus polyploid) to endangerment and invasiveness. We also related chromosome number (absolute number and relative to the minimum recorded for the genus) to endangerment and invasiveness with a randomization test, taking the variation of reported chromosome numbers into account. All analyses considered the relatedness of the taxa.

3. We found that endangered plants are disproportionately likely to be diploid and to have lower ploidy ratios, whilst invasive plant species are generally found to have high chromosome counts and to be polyploid.

4. While considering the effect of relatedness, being endangered is c. 8% less likely as ploidy ratio doubles and 14% less likely for polyploids compared with diploids. Being invasive is 12% more likely as chromosome number doubles and 20% more likely for polyploids compared with diploids. There was no significant effect of raw chromosome number on endangerment or of ploidy ratio on invasiveness.

5. Our findings demonstrate the importance of genomic attributes as risk factors of vulnerability to endangerment or invasiveness in higher plant species, and raise interesting questions as to potential causes of the pattern.

6. Synthesis. Our findings generate new hypotheses on plant rarity and invasiveness influenced by genomic attributes and further our understanding of the role of ploidy in rarity and invasiveness in higher plants. The cause of these relationships are potentially complex, requiring further research; ultimately, understanding the mechanistic basis of population status could aid conservation programs seeking to identify potentially endangered or invasive species.

Key-words: conservation, diploid, general linear mixed model, invasive aliens, invasiveness, phylogenetics, plant species, ploidy, polyploid, rarity

Introduction

The rarity or abundance of species has been of interest to ecologists and evolutionary biologists from the inception of the field (e.g. Darwin 1859, pp. 319–20), and the topic has gained in importance with time, especially with the growth of interest in conservation biology. It has long been known that rarity is itself a common phenomenon (e.g. Preston 1962); even in communities dominated by a few common species, the majority of species is usually found to be rare. Indeed in many biodiversity samples the modal abundance class is the rarest one (e.g. Novotny & Basset 2000). On the other end of the abundance spectrum, there has been a recent growth in interest in species that threaten to become too common in particular non-native taxa that come to dominate their new communities. While most alien species remain relatively rare in their introduced ranges (Williamson & Fitter 1996), a subset of them, commonly termed ‘invasive aliens’ (Colautti & MacIsaac 2004), expand their numbers to the point that they threaten profound ecological and/or economic impacts.

There has been considerable research interest in recent years in developing predictions of what attributes of species
predispose them towards becoming invasive (e.g. Rejmanek 1996; Stohlgren & Schnase 2006). Indeed, it has been argued (Bradshaw et al. 2008; Blackburn & Jeschke 2009) that rarity and invasiveness may be thought of as two extremes of a continuum, so that contrasting values of the same set of traits may be expected in the two groups.

If we are to manage rare or invasive species’ populations effectively, we need to understand the reasons they have become rare or invasive and the ecological and evolutionary consequences of that status. A steady stream of papers over the years has compared the traits of rare and common species (reviewed in Kunin & Gaston 1993; Gaston & Kunin 1997), and many have recorded overlapping but statistically differentiable sets of traits amongst rare and common species (e.g. Thoevarides & Dukes 2007; Milbau & Stout 2008). Whatever their origin, knowledge of likely trait differences between rare and common species can help guide the assumptions of conservation planners when (as is often the case for rare species) gaps exist in our knowledge of species of conservation concern. Similar issues have arisen in comparing the traits of invasive and non-invasive species (e.g. Hamilton et al. 2005; Muth & Pigliucci 2006), as any consistent trait differences might prove useful in predicting the invasion risk associated with different alien species, and thus could help guide biosecurity policy or control efforts.

Rare and common species have been found to differ in a range of ecological traits. It is notable, however, that most of these ecological comparisons are noisy at best, and there are clear exceptions to almost all of the proposed trends (Bevill & Louda 1999). A similar litany of trends and exceptions could be made for invasive species (e.g. Williamson & Fitter 1996; van Kleunen, Weber & Fischer 2010). In addition to the ecological traits noted above, there are also genetic and phylogenetic correlates of rarity and invasiveness. For rarity, the best known genetic correlate is a decreased level of genetic diversity (e.g. Karron 1987; Sherman-Broyles et al. 1992), presumably linked to the inbreeding and genetic drift inherent in small, isolated populations. Certain families have been reported to contain disproportionate numbers of rare species, suggesting heritable tendencies towards rarity (Edwards & Westoby 2000; Cadotte & Lovett-Doust 2002; Wild, Gagnon & Bouchard 2006), although the specific families involved are not always consistent across space. Similar taxonomic biases have been reported amongst invasive species (e.g. Richardson & Rejmanek 2004). Taxon size and evolutionary antiquity have also been suggested as factors associated with rarity (Hodgson 1986; Schwartz & Simberloff 2001; Lozano & Schwartz 2005). Here again, various studies have sometimes yielded conflicting results. For example, being evolutionarily ‘advanced’ and having a large number of species within a family was initially found to be negatively correlated with frequency of rare species in the Sheffield flora (Hodgson 1986), but a subsequent investigation of the same region using similar statistical analyses could not establish a link between these factors and proneness of taxa to rarity in the same habitat (Schwartz 1993).

As ecological and biological attributes have not yielded clear cut patterns in plant rarity, some researchers have turned to genetic and genomic traits in understanding patterns of rarity in plants (Vinogradov 2003; Pandit 2006; Pandit, Tan & Bisht 2006). For example, one of the studies suggested that increased DNA C-values are positively correlated with risk of extinction (Vinogradov 2003). Another study conducted on endangered plant species of the Indian subcontinent showed a strong link between ploidy levels on the one hand and both rarity and invasiveness on the other, concluding that diploid plants were more likely to be rare than polyploids, and that increasing chromosome number was negatively correlated with the probability of endangerment (Pandit 2006). In a related study, the authors showed that the highly invasive plant species in Singapore were all polyploids (Pandit, Tan & Bisht 2006). Another recent study of a single genus (Clarkia) confirms the relationship between ploidy and range size (Lowry & Lester 2006), and an even more narrowly focussed study (Treier et al. 2009) shows how polyploidy has increased within the invasive range of a single species (Centaurea maculosa). The link between polyploidy and invasiveness has been suggested in the literature (Hodgson 1987; Soltis & Soltis 2000; Lee 2002), but the association of diploidy with rarity (Lowry & Lester 2006; Pandit 2006) was hitherto unknown.

It is worth highlighting here that the majority of the studies have focused on only small sets of species, or at most, on regional floras and relatively restricted sets of habitats, in order to prioritize ecosystem targets for conservation (Schwartz 1999). Hence, the results from such studies may not be reflective of the correlates of rarity or invasiveness among species in general, as different factors could have variously pronounced effects on species survival or invasiveness in different regions or habitats. It is, therefore, important to consider data from wider geographic regions and heterogeneous habitats. In this study, we have attempted to search for a pattern among globally endangered and invasive plants by analysing the relationship between their ploidy levels and chromosome numbers and their conservation status. We specifically tested the hypothesis that endangered species are more likely to be diploid than polyploid, and that invasive plants were more likely to be polyploid than diploid. It is hoped that the relationship between ploidy and plant conservation status can be strengthened by our global study, leading to a greater understanding of this association.

Materials and methods

Data sources

We tested the relationship between species status (endangered or not, and invasive or not) with two measures of chromosomal state: ploidy level and chromosome number within a global data set of angiosperm species. We used categorical descriptions of species status (e.g. endangered/non-endangered, invasive/non-invasive) rather than more sensitive continuous measures (e.g. global population size or rate of change) because such categorizations are readily available for a much wider species set, and because they serve as useful summary variables for a range of interlinked variables (e.g. for rarity: global geographic range, number of populations, size or density of populations and population trajectory; see Mace & Lande 1991; Mace et al.
2008). For endangered species we considered those taxa that are listed by the IUCN (IUCN 2007) or Germplasm Resource Information Network, USDA (GRIN, 2006; specifically in GRIN we considered endangered species as those that are listed by the Center for Plant Conservation, classed as Endangered or Threatened Species by the U.S. Fish and Wildlife Service or in Appendices I and II of the Convention on International Trade in Endangered Species. For the invasive species we considered those listed in the Global Invasive Species Database (http://www.isg.org/database). For each species we obtained chromosome numbers from Fedorov (1969); Kumar & Subramaniam (1985) and online sources such as IPCN (http://mobot.mobot.org/W3T/Search/ipcn.html) and Royal Botanic Gardens Kew Database (Bennett & Leitch 2005, http://data.kew.org/cvalues/CvalServlet). For our non-endangered and non-invasive species sets, we included in our data set congeners of each endangered and invasive species for which we could obtain information on chromosome number. This is akin to a sister taxon analysis and so we are ‘making comparisons within sets of closely matched taxa rather than between them’ (Purvis 2008). We only included an endangered or invasive species in our analyses if we were able to obtain chromosome numbers for the species itself and at least one of its congeners.

PLOIDY

We considered three measures of ploidy in our analyses: raw chromosome number (from the sources cited above), ploidy ratio (the ratio of a species’ chromosome number to the minimum chromosome number reported for that genus) and ploidy category (diploid or polyploid). We defined ploidy category as described in standard cytogenetic literature to include minimum somatic chromosome reported for the species as diploid and any upward variation from that number indicated by duplication of a set of chromosomes (aneuploidy) and/or whole genome duplication (euploidy) as polyploid. In practice, we defined polyploids as species for which the maximum reported chromosome number was 1.5 or more times the minimum reported for that genus. We note therefore that our assessment of ploidy only considered recent chromosomal rearrangements and we could not include ancient and periodic episodes of recombination, and chromosomal rearrangements resulting in polyploidization.

DATA ANALYSIS

Often there was more than one chromosome number reported for each species. We could not use the most frequently reported chromosome number because this information was not available for most species. Instead, for our analyses of the relationship with chromosome number and ploidy ratio, we used a randomization test. In this test, performed with code that we wrote in R using the function ‘sample’ in the base package, we randomly selected one of the reported chromosome numbers for each species in turn, ran the analysis to obtain the summary statistics and then repeated the process a total of 1000 times. For each iteration of the randomization test we recorded the estimated effect size and its variance. We then calculated the mean effect size and its total variance (according to the ‘law of total variance’: the mean of variances from each iteration added to the variance of the means) and from this calculated the significance of the difference from zero of the effect size with a Z-test. In contrast to our randomisation test, other similar studies on chromosome number might consider either maximum or minimum chromosome numbers (i.e. simple definitions of ploidy). For comparison with these studies, we report analyses of our data set considering the maximum and minimum chromosome number reported for each species (see Appendix S1 in Supporting Information).

PHYLOGENETIC ANALYSIS

Rare species are not randomly distributed in phylogenies (Edwards & Westoby 2000; Cadotte & Lovett-Doust 2002; Wild, Gagnon & Bouchard 2006) and we expect that the same is true for invasive species (e.g. Richardson & Rejmanek 2004); therefore it was essential to take account of phylogenetic relatedness in our analyses. A fully phylogenetic approach, incorporating an appropriate level of phylogenetic correction, is the best way of including such information in analyses (Freckleton, Harvey & Pagel 2002; Duncan, Forshy & Hone 2007). When the dependant variable is binary, this can be performed using either generalized estimating equations (GEE; Paradis & Claude 2002) or phylogenetic logistic regression (Ives & Garland 2010). We attempted to use GEE for our analysis but the huge size of our data set meant that the models were unable to run successfully. Therefore in all our analyses we adopted an approach that is less computationally intensive, albeit not fully phylogenetic: that of a general linear mixed model (GLMM) with taxonomic information as nested random factors and with binomial errors (for a similar example, but with Poisson errors, see Phillimore et al. 2007). We tested the variation due to genus, family, order and a higher level that was based on the main groupings in the Angiosperm phylogeny (Angiosperm Phylogeny Group 1998) and included the relevant levels in the GLMM. Endangered or invasive taxa at subspecies level were treated as equivalent to full species in all analyses. Chromosome number and ploidy ratio were log2-transformed before analysis (this means that a unit increase in the transformed value represents doubling of the original value).

GEOGRAPHIC SPREAD

Information on endangerment came from two sources (IUCN and GRIN); the geographic spread of rare species from IUCN was: 28 from Europe, 21 North America, 3 South Africa, 34 Southeast Asia and that from GRIN was: 53 from Africa, 64 Asia-Tropical, 48 Asia-Temperate, 23 Europe, 64 Pacific, 300 North America, 35 South America and 51 whose distribution was not recorded by the database. Therefore, we tested for differences between the two sources and geographic regions in the species listed in the IUCN to test for potential bias in our data. Specifically, we tested the effect of source of data and region on log-transformed maximum reported chromosome number for each rare species, with genus nested within family as a random factor.

All analyses were carried out with multilevel models (i.e. general linear mixed models) using the function ‘lmer’ in the package ‘arm’ 1.3 (Gelman & Hill 2006) within R 2.8.1 (R Development Core Team 2008).

Results

We obtained chromosome data on 640 endangered species and 9005 congeners in 227 genera in 81 families in 30 orders of flowering plants. We also obtained chromosome data on 81 invasive species and 2356 congeners in 70 genera in 40 families in 21 orders. These taxa were well-distributed in the angiosperm phylogeny. In our data set the total number of species per genus ranged from 2 to 484 (median = 17) for endangered and from 2 to 304 (median = 8) for invasive species. The
number of endangered species per genus ranged from 1 to 96 (Euphorbia) and invasive species per genus ranged from 1 to 4 (Rubus); for both sets the median was 1. We obtained chromosome data on between 304 and 0.1 non-endangered congeners per endangered species (median = 9; note that the minimum of 0.1 was when there were nine endangered species and one non-endangered congener in a genus) and 303 to 0.5 non-invasive congeners per invasive species (median = 7). Of the endangered species for which we could obtain data on chromosome numbers, 554 were from GRIN and 86 were from IUCN. Of 2239 threatened species on the IUCN red list, the chromosome numbers were available for only 86 species. Of the 120 species on the Global Invasive Species List, we were able to obtain chromosome numbers for 81.

There was substantial variation in the number of reported chromosome numbers: just five of the endangered species (0.8%) had two reported chromosome numbers (and none had more than two), while 30.6% of invasive species had more than one reported chromosome number, with a maximum of ten reported chromosome numbers per species. These differences are so substantial that the difference is likely to be real even though it will be exacerbated by reporting bias (each invasive species being more likely to be intensively studied than each endangered species). In comparison, 15.8% and 14.2% of the congeners of endangered and invasive species, respectively, had more than one reported chromosome number.

Having accounted for genus nested within family in the analysis of our results from the randomization test, we showed that, first, increasing chromosome number is associated with a non-significant decrease in the probability of being endangered and a significant increase in the probability of being invasive (Fig. 1; Table 1). Secondly, increasing the ploidy ratio (chromosome number relative to the minimum reported for the genus) is associated with a significant decrease in the probability of being endangered and a non-significant increase in the probability of being invasive (Fig. 1; Table 1). Lastly, taking account of the relatedness of species within the data set showed that being polyploid compared with diploid caused a significant decrease in the probability of being endangered and a significant increase in the probability of being invasive (Fig. 1; Table 1).

Fig. 1. Graphical results of the randomization test. Histograms show the frequency of results of the coefficient of the main effect (β) from the randomization tests and, for comparison, the coefficients of the main effect when considering the maximum and minimum reported chromosome numbers (see Appendix S1). Chromosome numbers and ploidy ratios were log2-transformed before analysis. Class sizes for the histograms are 0.002 for endangerment and 0.02 for invasiveness. An effect size of zero is indicated by a dotted vertical line.
chromosome number doubles, 8% less likely as ploidy ratio doubles and 14% less likely for polyploids compared with diploids. Being invasive is 12% more likely as chromosome number doubles, 1% more likely as ploidy level doubles and 20% more likely for polyploids compared with diploids. The difference of genera (nested within families) from each other was about ±40% on the probability scale, while families differed by about ±5%.

Across our GLMM analyses we consistently found that the majority of the taxonomic variation was due to genus, a smaller amount was due to family (Table 1). Initial analyses with genus and family nested in either order or higher taxonomic levels demonstrated that negligible variance (< 0.0001) was explained by levels higher than family, so these were not included in our analyses presented here. For endangered species there was no variation due to source of data (GRIN or IUCN: \( P = 0.379 \)) or region for species listed by the IUCN (\( P = 0.091 \)).

**Discussion**

Unravelling the links between species traits and rarity and invasiveness is a highly complex task because of the impracticality of performing controlled experiments at evolutionary and biogeographic scales. This impediment, to a great extent, can be overcome by using widely accessible databases and analytical models. We have assembled the largest data set to date for testing the potential association between ploidy and plant population status (endangerment or invasiveness), using a range of different approaches to ensure robustness. Overall, while some differences are found between the details of the different approaches, our results demonstrate a clear pattern: endangered plants are disproportionately likely to be diploid and to have lower ploidy ratios (although they were not significantly lower in their raw chromosome counts), whilst invasive plant species are generally found to have high chromosome counts and to be polyploid (expressed in categorical terms, despite the lack of significant patterns in terms of ploidy ratios). This confirms the generality of the findings of the studies restricted to small geographical area by Pandit (2006); Pandit, Tan & Bisht (2006); Lowry & Lester (2006). The size of the effects was often substantial, suggesting that cytology has a surprisingly strong association with population status.

It is not uncommon for multiple chromosome values to be recorded for a single species, and it takes a further interpretive step to deduce ploidy levels from chromosome counts. We employed randomization tests amongst reported chromosome counts, so as to overcome the clear biases that would have resulted from employing either minimum or maximum reported values (see Appendix S1). This provided clear statistical distributions of chromosome counts for each focal species set (see Fig. 1), thus allowing a clear interpretation of overall trends despite the ambiguity in ascribing chromosome numbers at the individual species level. These same randomization techniques were employed to consider the effects of ploidy as a continuous variable (ploidy ratio), but a categorical measure of ploidy was also considered using a binary analysis. While the results of these three approaches were not always consistent in detail, the differences between them can prove instructive. For example, our results suggest that chromosome number *per se* does not substantially affect risk of endangerment, but that risk of endangerment is associated with the chromosome number relative to congeners (ploidy ratio or ploidy category in Table 1). In our randomization test, we assumed that each of the reported chromosome numbers was equally prevalent for each species. Although this is unlikely to be the case for all species, we also consider that the randomization test is the best estimate of the true effect size, avoiding the demonstrable biases associated with considering the maximum or minimum reported chromosome numbers (see Appendix S1). In this large-scale analysis, we were also unable to consider situations in which, for example, a species is diploid in much of its native range, but polyploid as an invasive in non-native ranges (Lafuma et al. 2003; Treier et al. 2009). It is possible that our results may be partly due to sampling biases: all other things being equal, better studied species will have a larger number of chromosome numbers reported. However, the overall results are sufficiently strong and robust that we are confident that the results are realistic.

We found substantial variance due to taxonomic level which was greatest at the genus level and decreased with increasing taxonomic level (Table 1), confirming our expectation that we

**Table 1. Relationship of endangerment and invasiveness with chromosome number and ploidy level, as inferred from the minimum chromosome number recorded for each genus. The results of chromosome number and ploidy level are from a randomization test as described in the text**

<table>
<thead>
<tr>
<th>Dependant variable</th>
<th>Main effect</th>
<th>Main effect size (( \beta ))</th>
<th>( P )-value</th>
<th>Odds ratio*</th>
<th>Variance due to genus, family†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Endangerment</td>
<td>( \log_2 ) (chromosome number)</td>
<td>-0.074</td>
<td>0.376</td>
<td>0.929</td>
<td>1.659, 0.254</td>
</tr>
<tr>
<td></td>
<td>( \log_2 ) (ploidy ratio)</td>
<td>-0.308</td>
<td>&lt;0.001</td>
<td>0.735</td>
<td>1.513, 0.199</td>
</tr>
<tr>
<td></td>
<td>Ploidy category</td>
<td>-0.546</td>
<td>&lt;0.001</td>
<td>0.579</td>
<td>1.528, 0.167</td>
</tr>
<tr>
<td>Invasiveness</td>
<td>( \log_2 ) (chromosome number)</td>
<td>0.489</td>
<td>0.016</td>
<td>1.624</td>
<td>0.971, 0.359</td>
</tr>
<tr>
<td></td>
<td>( \log_2 ) (ploidy ratio)</td>
<td>0.049</td>
<td>0.821</td>
<td>1.050</td>
<td>0.911, 0.455</td>
</tr>
<tr>
<td></td>
<td>Ploidy category</td>
<td>0.784</td>
<td>0.009</td>
<td>2.190</td>
<td>1.252, 0.450</td>
</tr>
</tbody>
</table>

*The odds ratio (calculated as \( e^\beta \)) gives the change in odds of being endangered or invasive for a unit increase in the main effect (a unit increase being a doubling in the original value for \( \log_2 \)-transformed variables and change from diploid to polyploid for ploidy category).†There was little variation across the 1000 iterations for the variance in the random effects in the analyses of chromosome number and ploidy ratio, so here we present the mean.
needed to consider relatedness of species in these analyses. The GLMM was the only approach currently available to relate binary variables to independent variables while taking account of phylogenetic relationships. Although it has the disadvantage of treating species within a genus as being independent (a problem highlighted by Purvis 2008), we expect this effect would have been minor. Including fully resolved phylogenetic information in this logistic regression (Paradis & Claude 2002; Ives & Garland 2010) would have been ideal, but we were unable to run these models successfully with our data. This was due, apparently, to computational limits with our very large sample sizes, despite the very large sample sizes being a strength of our study. Our findings could have a positive impact on how plant species are selected and prioritized for conservation (Kunin & Gaston 1993), and conversely on the threat that they pose as potential invasives (Pandit & Inderjit, unpublished data). It is hoped that studies such as this will provide the impetus to uncover the reasons behind this genetic association.

In the context of ploidy and chromosome number, rarity or invasiveness may be a synergistic outcome of entry and transformation biases (Kunin 1997); that is to say: abundance may affect ploidy, and conversely ploidy may affect abundance. Entry biases would occur if rare species were disproportionately likely to be diploid, or rather, if we assume diploidy to be the ancestral state, if common species (and we consider that invasive species are likely to be common) were disproportionately likely to become polyploids. This might occur because the commoner a population, the more individual reproductive events there are in which the rare events of chromosome doubling could occur. The more such occurrences, the better the chances of a polyploid population persisting and becoming established, rather than being weeded out by chance or frequency-dependent selection. A great deal has been written about polyploidy and its advantages to plant species from expanding their potential geographic distribution to reducing susceptibility to inbreeding depression (see Soltis & Soltis 2000). In a competitive world, the natural corollary is that diploidy may prove disadvantageous, both ecologically and evolutionarily. The suggestion that diploidy may restrict adaptive evolution (Pandit 2006) needs further empirical investigation.

The transformation biases, on the other hand, operate in the opposite direction: being polyploid may not just occur as a consequence of commonness, it may help make species common, hence diploids are less likely to become common and so become endangered due to small and/or fragmented populations. There are thought to be a number of physiological and ecological adaptations in polyploids (for reviews see Soltis & Soltis 2000; Lee 2002) which collectively may contribute to species becoming common or invasive. These adaptations can lead to competitive dominance; some studies show that polyploids produce nearly 100% of the biomass in certain habitats, leaving little space for less common diploid species (Pandit, Tan & Bisht 2006). The continued presence of nearly 30–50% diploid species among the global flora as a whole (see Soltis et al. 2009), however, indicates their effective persistence, despite this apparent competitive disadvantage. Recent evidence, based on cytological, fossil and genome data, suggests, however, that angiosperms might have undergone more than one event of polyploidization and that there could be 47–100% polyploids among higher plants (Wood et al. 2009). This interesting observation could, to a large extent, explain the persistence of diploids, which may in fact have undergone polyploidization in the past. There is very little experimental evidence available at this point that could effectively explain the prevalence of polyploidy amongst common and (particularly) invasive species. Recent comparative studies (Chen, Guo & Yin 2010) and experimental studies on Phlox drummondii, Solidago gigantea and Arabidopsis spp. (Vyas et al. 2007; Hull-Sanders et al. 2009; Ni et al. 2009) have shown that polyploids have a distinct advantage in photosynthetic efficiency, growth, reduced generation time, vigour and biomass over their diploid counterparts, but whether this or similar advantages are found more universally amongst polyploids is not known.

Much of the literature on invasiveness implicitly presupposes that polyploidy affects invasiveness; the added vigour conferred by polyploidy can provide an opportunity for invasiveness. For example, it was found that many noxious weeds are allopolyploid hybrids (Blair & Hufbauer 2009; Schierenbeck & Ellstrand 2009) and polyploid hybrids demonstrated increased heterozygosity and hence were better equipped to deal with inbreeding depression, making them more dominant than non-invasives (Soltis & Soltis 2000). The success of invasive species has also been attributed to their flexibility in behaviour and penchant for mutualistic interactions (Mooney & Cleland 2001). However, until recently there has been little evidence to justify the assumption that polyploidy affects invasiveness; it is equally plausible that the rapid expansion and successive genetic bottlenecks experienced in the process of invasion create selective pressures favouring polyploidy. There is increasing evidence that the ‘invasive’ traits of invasive species may evolve at least in part in response to conditions experienced during invasion (Whitney & Gabler 2008); whether this holds for ploidy, however, is unclear. The fact that polyploidy might arise in response to environmental stress such as extreme temperature, high salinity, injury through herbivory, radiation, herbicide use, etc. proffers adaptive advantage against these very selection pressures (see Ramsey & Schemske 1998; Hase et al. 2006). The best empirical evidence to date of polyploids as invasives comes from a recent study of an invasive species (Centaurea maculosa) that has both extensive diploid and tetraploid populations in its native European range, and while both diploids and tetraploids were introduced to North America, the populations there are now almost exclusively tetraploid (Treier et al. 2009). These results show signs of both pre-adaptation (European tetraploids tolerate a wider range of climates than their diploid counterparts), but also of selective advantage in the process of invasive spread. The distinction between causes and consequences of invasion may not be as clear cut as might be supposed.

Genetic and genomic attributes of species can provide significant leads in understanding both the evolutionary history and potentially the future prospects of species. Our results suggest that the chromosomal status of many of these species may play a part in explaining their current status. As such they may be
of use in guiding management decisions concerning endangered species as well as for potentially invasive taxa. However, there is still a general lack of cytological data among plant species, and some endangered species may have become extinct even before their cytological status is known (Pandit 2006).

Conservation biologists, so far, have searched to decipher patterns in the species traits associated with rarity based on ecology and taxonomy. The present study, however, provides evidence of genomic correlates of both rarity and invasiveness that hold across wide ranges of taxa in a global analysis. This study provides evidence that rarity and invasiveness, which form opposing ends of a species trait spectrum, show associations with diploidy and polyploidy, respectively. A large majority of the higher plant species, particularly the endangered species, have not been cytologically investigated, limiting the ability of this association to help potentially identify species at risk of becoming endangered. At present, there is no mechanism explaining the correlation between diploidy and rarity except that diploidy may be acting as a restrictive control on the fitness of species, thereby affecting persistence and divergence. However, this association should be further investigated to determine potential mechanisms resulting in endangerment.

For invasive species, there has been increasing demand, as global trade increases, for the development of risk-assessment methods for judging the potential invasiveness of alien species in novel environments (e.g. Stohlgren & Schnase 2006). Our results suggest that ploidy levels may be a useful component in such assessments. We suggest that cytological investigations of rare and invasive species be taken up as a priority, for the potential benefit of conservation and invasion biology.

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Supporting Information

Additional supporting Information may be found in the online version of this article:

**Appendix S1.** Relationship of maximum and minimum reported chromosome number with endangerment and invasiveness.

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