Searching for patterns of extinction risk in three sections of *Gladiolus* (Homoglossum, Hebea and Heterocolon) in southern Africa

In partial fulfillment of my Botany Honours Degree

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Abstract

The aim of this study was to search for patterns of extinction risk across phylogenetic, ecological and life history traits of *Gladiolus* in southern Africa. The extent to which certain traits may contain an unexpected number of threatened individuals was assessed by the departure from a normal hypergeometric distribution. In addition I tested whether the 'extinction risk model' developed by Bond (1994) could be applied to predict risk across life history traits. Besides an unexpected number of threatened species occupying an inundated habitat ($p = 0.02$), there were no clumping effects over any of the traits analysed. I suggest that the observed random distribution of threatened species is indicative of a genus which occupies a diverse range of niches with few members in each.

Introduction

A number of previous studies have searched for patterns of extinction risk within a group of organisms (Hodgson, 1986; Shwartz, 1993; Bennett and Owens, 1997; Hegde and Ellstrand, 1999; Lockwood *et al.*, 2002; Symonds, 2002; Pilgrim *et al.*, 2004). While the variables used vary greatly, it can be generally inferred that all studies seek correlations between extinction risk and one/a combination of the following: phylogenetic relationships, life history and ecology.

Phylogenetic correlates

There is now evidence to suggest (Schwartz, 1993; McKinney *et al.*, 1996; Owens and Bennett, 2000; Purvis *et al.*, 2000; Lockwood *et al.* 2002) that often, rare species are clumped within certain taxonomic groups. Owens and Bennett (2000) showed that among bird families, parrots, pheasants and albatrosses (to name but a few) contained significantly more threatened species than expected. While in a broader study, Lockwood *et al.* (2002) showed that clustering of extinction threat occurred predominantly at the level of family and genus among vertebrate species in the U.S.

A significant correlation between extinction risk and phylogeny suggests that extinction risk (or extinction in the extreme) may be the result of inherited characteristics (Pilgrim *et al.*, 2004). This has profound implications for conservation efforts, since if extinction risk is unusually clumped within a higher taxon, then special attention should be paid to the group of species within it that are not presently threatened as these species may have a higher chance than expected of becoming threatened (Lockwood *et al.*, 2002). Taxonomic patterns therefore, might enable conservationists with limited resources and funds, to become more focused and proactive (Lockwood *et al.*, 2002).

Ecological Correlates

The first studies to search for patterns of extinction risk, focused mostly on ecological parameters. For instance in an extensive study of British flora by Hodgson (1986), rare species were often associated with less fertile areas, ranging from land subject to changes in use because of agriculture to undisturbed habitats with a high species richness. As was the case for agriculture in Britain, ecological correlations are useful in that they often serve to highlight types of human disturbance that cause the greatest amount of damage.

When searching for ecological traits that confer extinction risk, it is important to account for the fact that related species occupy similar habitats (Harper and Clatworthy, 1963) and therefore heritability of threat would confound a non-phylogenetic test (Pilgrim *et al.*, 2004). In Pilgrim *et al.*'s (2004) study of native British flora, the effect of inheritance was mitigated by examining each ecological trait that possessed more rare species than expected and removing any sizeable groups of threatened congeners before repeating the analysis. In analyses such as this, it has been shown that using an accurate phylogenetic topology rather than an approximate taxonomic one can increase the accuracy and robustness of test results (Symonds, 2002).

Pilgrim *et al.*'s (2004) study is also an excellent candidate to highlight the importance of incorporating in the same study searches of both phylogenetic as well as phylogenic-independent data for patterns of extinction risk. Although Pilgrim *et al.* (2004) found significant clustering of threatened species among orders of angiosperms, in light of a stronger correlation to habitat type, they made the following recommendation: '*for British flora local conservation efforts might be better targeted by habitat rather than taxonomically. Although at a global scale (K. Dolphin unpublished data) some families are significantly more prone to threat than expected, the same was not true for Britain, where habitat was a better predictor even within taxa identified as threatened.*'

Life history correlates

Many recent studies have attempted to predict a taxon's predisposition to extinction risk by analyzing species' traits across phylogenies (Schwart, 1993; McKinney *et al.*, 1996; Owens and Bennett, 2000; Purvis *et al.*, 2000). For example, Owens and Bennett (2000) found that once phylogeny had been controlled for, increases in extinction risk were independently associated with increase in body size and decreases in fecundity in birds. They used this trend to identify key species which posses a low probability of recovering if human disturbance perturbs the natural balance between fecundity and mortality.

However, methods that analyze species' traits across phylogenies are complex and require an accurate phylogenetic topology (Symonds, 2002). Hence, in this study I make use of an alternate approach proposed by Bond (1994) which, attempts to predict extinction be examining relative dependencies on mutualistic relationships between plants and their pollinators and dispersers. As Bond (1994) explains, '*these reproductive mutualisms epitomize the subtle, complex web of interactions, which if broken by human actions, could cause a cascade of extinctions*'.

In this approach, species can be rapidly ranked based on three criteria namely:

1. *The probability of a mutualism failing*. With a high risk of failure resulting from a dependence on a single species for pollination and obligatory dispersal to cue germination. While self pollinated and wind dispersed species resulting in low risk.

2. *The degree of reproductive dependence on mutualism.* With asexual species possessing no risk and species which are self-incompatible or dioecious possessing high risk.
3. *The importance of seeds in the demography of the plant.* With vegetatively propagated species possessing a low risk and short lived species that lack a seed bank and are killed by disturbance possessing a high risk.

Application of extinction risk patterns – general vs. local

Occasionally, extinction risk patterns are general in character and therefore hold the potential of being broadly applicable. For example, Hegde and Ellstrand (1999) statistically compared life history traits of rare and common vascular plants in two better –studied but climatically and geographically distinct Holarctic floras – those of California and Britain, and found trends (example woodiness) that were common to both. Furthermore, Pilgrim *et al.* (2004) cite unpublished data, which shows that certain families of vascular plants are significantly more prone to threat than expected (they identify cacti and palms among many others) on a global scale.

However, in other instances when additional studies were preformed to test the validity of a extinction risk pattern in a new area, no significant correlation could be found. In a study by Schwartz (1993) the correlation between rare plants and primitive plant families that has been shown for the flora of Sheffield Great Britain (Sporne, K.R., 1980) was tested in regions of North America. While Schwartz, could show some taxonomic affiliations with extinction risk, degree of primitiveness was unable to predict these affinities, suggesting that Sporne's (1980) study was not generally applicable. As a result of local variation in extinction risk patterns, there is a clear need for independent studies in a broader range of conservation sites.

Extinction risk assessment of *Gladiolus* in Southern Africa

Gladiolus is the largest genus of the petaloid monocot plant family Iridaceae, and is thought to comprise some 255 species (Goldblatt and Manning, 1998). Southern Africa (with 163 species) forms the center of the genus in terms of both species richness and overall diversity. *Gladiolus* is regarded as a highly diverse and successful genus. Its success is attributed most notably to the following:

1. Unusual floral adaptability that over time has allowed species to become specialized for almost all the important floral pollinators in Africa.
2. Vegetative specialization
3. Variation in leaf morphology has permitted radiation from moist, high-rainfall to semi-arid sites.
4. Various species in the genus are adapted to grow on most of the substrates encountered here in Southern Africa.
5. Other significant adaptations are the ability to flower after the season's leaves have withered and before the next season's vegetative shoot has sprouted
6. Control of the flowering response
7. The specialized, wind-dispersed seeds have enabled the genus to spread widely and to colonize isolated and disjunct habitats in which populations may diverge and evolve into new species largely as a result of their geographic isolation (Goldblatt and Manning, 1998).

This vast array of ecological and life history traits makes *Gladiolus* an interesting case study in which to explore patterns of extinction risk. The aim of this study is to analyze a meaningful subset of these traits within the context of the genus's phylogeny to elucidate patterns of extinction risk. It is my hope that this study will help direct the conservation efforts centered around *Gladiolus* in southern Africa.

Methods

Data Collection

Risk parameters (phylogenetic, ecological, life-history) were collected for 61 *Gladioli* species in South Africa. These species represent a full appraisal of three *Gladioli* sections; *Hebea*, *Homoglossum* and *Heterocolon* with the exception of a handful that were discarded based on insufficient data. All 61 species from across these three sections were classified as either least concern (LC), near threatened (NC), vulnerable (V), endangered (E) or critically endangered (CE) in accordance with the criteria defined by the Interim IUCN Red Data Book of South Africa (1995), which makes assessments on the basis of population decline and range size. For the purpose of this study, however I classified all species that occurred within this database as threatened.

Ecological information about the *Gladioli* species under study was collected from Goldblatt and Mannings book entitled '*Gladiolus* in Southern Africa' (1998). Based on the 'distribution and biology' description within this book, I assigned each species to one of four habitat types and one of five soil types (table 1 and 2).

Table 1.
The number of *Gladioli* species found within each habitat category.

Habitat category	Number of Species	Number of threatened species
Inundated	0	6
Arid	2	3
Rocky	10	8
Other	17	15

For the purpose of this study a species occurring in woodland, renosterveld, fynbos, grassland, and karroid shrub was assigned to the 'other' categories due to the small number of species assigned to them.

Table 2.
The number of *Gladioli* species found within each soil type.

Soil type	Number of Species	Number of threatened species
Sand	11	11
Shale	1	4
Clay	4	6
Dolerite	0	1
Mixed	13	10

For the purpose of this study a species occurring in more than one soil type was assigned to the 'mixed category'.

The phylogenetic topology I used to define sections was hand constructed by Goldblatt and Manning (1998). This morphological phylogeny is based on the cladistic philosophy of Hennig (1966) in which relationships are assessed using only shared derived characters, i.e. synapomorphies.

Is threat randomly distributed across the *Gladioli* phylogeny?

The null hypothesis that the observed and expected values for the proportion of threatened species across the three sections was assessed using a chi-squared test.

Do any sections of *Gladioli* contain significantly more threatened species than would be expected by chance?

I used the hypergeometric distribution to identify sections with unexpectedly high numbers of threatened species in accordance with a study by Pilgrim *et al.* (2004). This distribution models the total number of successes within a fixed sample, drawn without replacement from a finite population. The 'hypergeometric distribution' function in the application JMP (SAS Institute, 2000) requires the imput of four variables, N, size of the population; K, number of items with the desired characteristic in the population, n, number of samples drawn, and x, number of successes in the sample. It returns the probability that x will be as small as it is. For example, when computing the probability that the section *Homoglossum* will have an expected number of species designated threatened, N, the total number of *Gladioli* species, K, the number of common *Gladioli* species, n, the number of *Gladioli* in the section *Homoglossum*, and x, the number of *Gladioli* in the section *Homoglossum* that are common. Hence, a small number of common species will return a small p value.

How are threatened species of *Gladioli* distributed across the various habitat categories in Southern Africa?

A χ^2 test was conducted to determine whether there was an uneven distribution of threatened species across habitat and soil types. For both the habitat and soil schemes, I then attempted to identify habitats and soil types; with more threatened species than expected under the hypergeometric distribution. This was done using the procedure outlined above. Additionally, a multiple regression was also performed in order to establish whether threatened species occur in areas with particular environmental variables or a combination of these variables. The environmental variables used were:

1. Maximum temperature
2. Soil moisture
3. Median rainfall
4. Evaporation
5. Solar radiation

In order to generate these variables I consulted the PRECIS database where I retrieved place descriptions of collected herbarium specimens. Using ARCVIEW I then identified the place of collection and hence determined a precise co-ordinate position. This was performed for approximately three herbarium specimens of each *Gladiolus* species. These co-ordinates were added to the precise co-ordinate data derived for the relevant *Gladioli* in ACKDATA. A climate envelope model (VegMap) was then used to assign species with environmental data values for those variables listed above.

Is threat correlated with variation in life history factors?

Life history parameters were selected on the basis of an extinction risk model proposed by Bond (1994). In this study by Bond (1994) the risk of plant extinctions were assessed by considering the probability of dispersal or pollinator failure, reproductive dependence and the dependence on seeds (Bond, 1994). The extinction risk model was reconstructed in this study in order to test whether it would accurately predict threat in *Gladiolus*. The axes of the model are identified as risk of reproductive failure in addition to seed dependence. Reproductive failure as described by Bond (1994) is the breeding system * pollination specificity. *Gladioli* are incapable of 'selfing' (Goldblatt and Manning, 1998) therefore a score of 1 for breeding system was assigned. I devised a rank system for pollination specificity based upon the level of dependence; hence in the case of butterfly-pollinated *Gladioli* where one butterfly species (*Aeropetes tulbaghia*) is responsible for the pollination of all species, I assigned a score of 1, which reflects its high risk to reproductive failure. Bee-pollinated *Gladioli*, on the other hand, are pollinated by a suite of bee species; I therefore assigned a score of 0.25 to reflect their generalist nature and low risk of reproductive failure (table 3).

Table 3.

Pollination specificity scores across the various syndromes.

Pollination Syndrome	**Subdivision (where applicable)**	**Score**
Bees	General	0.25
	Anthrophoridae	0.375
	Halictidae	0.375
Birds, Sunbirds		0.75
Long-tongued flies	General	0.5
	Nemestrinidae and *Tabanidae*	0.75
Moths, Hawkmoths		0.875
Butterfly		1

Sub-divisions are applicable where more than one group occurs within a syndrome.

Given that all *Gladioli* produce winged seeds of a similar size, seed dependence was assessed on the basis of corm structure. Corms that produce cormlets (clonal) are considered at low risk while single corms are potentially at a higher risk. However to give further resolution to this axis the size of the corms was also considered, due to the fact that a larger corm is thought to offer a higher chance of survival under predatory pressure. On the basis of these two factors a score was assigned (table 4).

Table 4.

Corm size and structure scores as a measure of seed dependence.

Corm size and structure	**Score**
Large clonal	0.25
Small clonal	0.5
Large single	0.75
Small single	1

Results

The taxonomic distribution of extinction threat among the *Gladiolus* species

It appears from the χ^2 test (table 5) that threatened species are randomly distributed across sections.

Table 5.

The Pearson Chi-square statistic of threatened status versus taxonomic sections.

Threat Level	χ^2	df	p
Status	3.99	2	0.14

Sections containing more threatened species than would occur by chance

Although not apparent in the χ^2 test, the hypergeometric test (table 6) identifies that an almost significant proportion of threatened species clump over the *Heterocolon* section ($p = 0.07$).

Table 6.
The p values obtained when comparing the distribution of threatened species across the *Gladioli* sections against a hypergeometric model.

Sections	Unexpectedly high number of threatened species
Hebea	0.92
Homoglossum	0.68
Heterocolon	0.07

Threat over habitat and soil types.

It is evident from the χ^2 tests (table 7 and 8) that threatened species are non-randomly distributed across habitats types yet randomly distributed across soil types.

Table 7.
The Pearson χ^2 statistic of threatened status versus habitat type.

Threat Level	χ^2	df	p
Status	8.72	3	0.03

Table 8.
The Pearson χ^2 statistic of threatened status versus soil type.

Threat Level	χ^2	df	p
Status	3.45	4	0.49

The hypergeometric test (table 9) identifies that the 'inundated' habitat type ($p = 0.02$) contains significantly more threatened species than expected.

Table 9.
The *p* values obtained when comparing the distribution of threatened species across habitat categories against a hypergeometric model (significant results are marked with *)

Habitat type	Unexpectedly high number of threatened species
Inundated	*0.02
Arid	0.55
Rocky	0.86
Other	0.88

As expected, the hypergeometric test across soil types yields no significant results (table 10).

Table 10.
The *p* values obtained when comparing the distribution of threatened species across soil categories against a hypergeometric model.

Soil type	Unexpectedly high number of threatened species
Sand	0.71
Shale	0.91
Clay	0.21
Dolerite	0.43
Mixed	0.52

Correlations of threat with environmental variables

No correlation between threat and environmental variation is apparent upon examination of the *p*-values obtained from the multiple regression analysis (table 11). In addition, the *p*-value for the combined correlation was not significant ($p<.60680$).

Table 11.

The *p* values obtained when comparing the distribution of threatened species across environmental variables using a multiple regression analysis.

Threat Level	**Beta**	t	*P*
Median Rainfall	0.05	0.25	0.8
Soil Moisture	0.26	0.84	0.40
Solar Radiation	0.24	1.06	0.29
Evaporation	-0.13	-0.52	0.6
Maximum Temperature	-0.3	-1.21	0.23

Correlations of extinction risk with variation in life history factors

It is suggested that the specificity and the degree of reproductive dependence, and the dependence on seeds, may compensate to reduce the risk of extinction (Bond, 1994). Hence, few species are hypothesised to occupy the high risk region (top right-hand corner) as extinction is likely to be responsible for their removal. This study, in contrast, depicts a number of *Gladioli* species occupying this region (figure 1). As proposed the majority of these species are classified as threatened, however, this does not account for two commonly distributed species found in this high risk region.

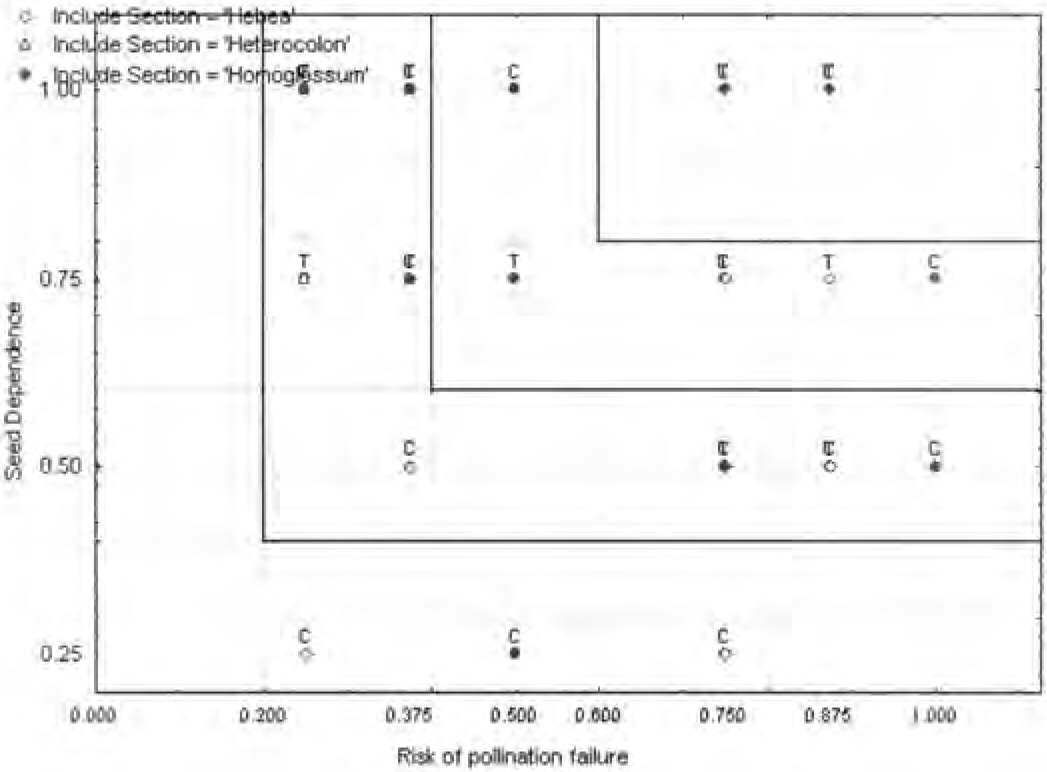

Figure 1. Threatened (T) and common (C) *Gladioli* species over the extinction risk model. Contours indicate proposed increased risk of extinction from the origin.

It is also apparent that of the *Gladioli* species that occur in the high risk region, the majority belong to the section Homoglossum (figure 1).

Discussion

The taxonomic distribution of extinction risk among the *Gladiolus* species

Although there is no significant clumping of threatened species across the taxonomic sections examined (table 5), *Heterocolon* demonstrates an almost significant departure from a normal hypergeometric distribution (table 6). Notable features of this small section that may contribute to their heightened extinction risk status include: adaptation to nutrient deficient quartzitic soils; and exhibition of limited floral diversification (Goldblatt and Manning, 1998). The latter as aforementioned (see Introduction) is uncharacteristic of the genus whose success is largely attributable to high floral diversification (Goldblatt and Manning, 1998).

The reason that no significant clumping of threatened species was observed across taxonomic sections might be explained by the fact that species may be threatened for disparate reasons, including human impact or association with a scarce habitat (Pilgrim *et al.*, 2004). However, before a lack of significant clumping over the *Gladiolus* phylogeny is taken as conclusive, an additional study should seek to construct a molecular phylogeny for the genus (at present there is none, communications with Manning 2005). This would allow for analyses such as *spatial autocorrelation* (which use extinction risks as a trait) to be conducted. This style of analysis was used by Lockwood *et al.* (2002) to search for taxonomic patterns of extinction risk in U.S. vertebrates. Their results serve to highlight that one cannot predict the taxonomic level at which clumping of threatened species occurs. In their study, they found that while amphibians showed a highly significant clumping of threatened species at the level of order, birds, on the other hand, display clumping at the level of family (Lockwood *et al*, 2002).

Correlations of extinction risk with ecology

A significant clumping of threatened species over habitat type (table 7) was followed by a hypergeometric distribution test which showed that only the inundated habitat type (table 9) displayed a significant departure from a normal hypergeometric distribution. This may be due to the fact that *Gladiolus* species found within inundated habitats (like *G. aquamontanus* and *G. sempervirens*) possess residual corms which may limit their ability to propagate vegetatively. In addition to this, water saturated environments are narrowly distributed sometimes having niche habitats as specific as cliffs or waterfalls (Goldblatt and Manning, 1998).

With regards to the clumping of threatened species over soil types (tables 8 and 10), no significant clumping was found. Seeing as most species of *Gladiolus* show strong edaphic fidelity (Goldblatt and Manning, 1998), this result suggests that for the sections examined soil type (table 2) does not critically limit the distribution of the species examined even though it is likely to define their range.

Caution should be taken not to extrapolated this result to sections that have not been examined. For example in section Ophiolyza, certain species are adapted to dolomite substrates which, have a limited distribution in southern Africa (Goldblatt and Manning, 1998). These highly localized species include *G. dolomiticus*, *G. macneilii* and *G. pavonia*. All three are classed as vulnerable and the latter two are know only from a single extended population (Goldblatt and Manning, 1998). Therefore, the inclusion of a section such as Ophiolyza might introduce significant clumping.

In my opinion, fire represents another important aspect of the ecology of southern African which, has been poorly addressed in studies of extinction risk to date. For geophytes in particular fire provides an important opportunity to produce flowers and seeds in the absence of competition from larger shrubs and trees (Goldblatt and Manning, 1998). While Goldblatt and Manning (1998), occasionally note where a strong relationship between fire and a particular species of *Gladiolus* exists, there has been no study to assess the relative dependency of each southern African *Gladiolus* species for fire. From the little that is known, one might assume that within *Gladiolus* the dependency on fire is highly variable. Ranging from specie like *G. phoenix* which is rarely seen except after a fire to *G. sempervirens* which grows in perennially damp sites and is so dependent on moisture that it's corm is vestigial. A logical extension of this study therefore would be to prepare a comprehensive list of *Gladiolus* dependency on fire across the genus and test whether a correlation exists between fire and extinction risk.

Correlations of extinction risk with life history

With respect to the extinction risk model (Figure 1) it appears that within *Gladioli* the compensation mechanisms (see results) proposed by Bond (1994) do not apply. This can be inferred by the fact that numerous species (both threatened and common) occur within the 'high risk region'. This is particularly evident over the 'reproductive failure axis' which, could be attributed to the fact that specificity to pollinators might in fact reduce extinction risk. Bond (1994), identifies an instance in which this trend occurs in 15 red-flowered species across four families (*Iridaceae, Orchidaceae, Amaryllidae* and *Crassulaceae*) in the Fynbos. These species were all highly dependent on a single butterfly species for pollination. The reduced risk was brought about due to the fact that pollinator feeding was almost exclusive for the plant species in question – resulting in considerable reliability (Bond, 1994).

The 'Seed Dependence' axis is a function of dispersal and dependence on seeds. However, seeing as *Gladioli* are all well adapted for wind dispersal (Goldblatt and Manning, 1998), perhaps the advantage conferred by my scoring of 'Seed Dependence' is negligible explaining the random distribution of species over the entire length of the axis.

Conclusion

In the case where a significant departure from a normal hypergeometric distribution was observed (table 9) a plausible explanation might be the conference of that trait to a narrow distribution. From this preliminary study, it appears that across *Gladioli*'s diverse range of ecological and life history traits their appears to be no pattern of extinction threat.

As Goldblatt and Manning (1998) suggested (see Introduction), perhaps it this very ability of *Gladiolus* to adapt to a diverse array of habitats that has made the genus so successful. For, if the niches occupied by *Gladiolus* are sufficiently diverse and at the same time only ever occupied by a few individuals, perhaps this phenomenon is sufficient to confound patterns of extinction risk.

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