Influence of flower colour and seasonality on plant invasion success

The ecological factors and mechanisms that determine the bioinvasion success of exotic plant species have become a *cause celebre* in current ecological research as witnessed by the many leading hypotheses and articles published[1–6]. In pursuit of understanding invasive plants, while mining the Global Invasive Species Database[7], we found that a large number of invasive plants are characterized by flower colour polymorphism and multi-seasonal flowering. An effort has been made here to find out if these two traits have any role in invasiveness in plants.

In the proposed hypothesis, we put forward an idea that plant species with flower colour polymorphism and multi-seasonality in flowering have a higher potential for bioinvasion success in introduced regions. To provide evidence, a list of 311 invasive species from the Global Invasive Species Database[7] was selected for the analysis. After data exploration on research articles and databases, 263 species with sufficient information on flower colour and seasonality were considered for the study. A list of 300 randomly selected plants from *The Flora of the Tamilnadu Carnatic*[8] (representing regional flora) and another 300 randomly selected plant species from 'Plant Trait Database'[9] (representing global flora) were considered separately for comparison of phenological traits with invasive plant species. The list of invasive and randomly selected flora at regional and global levels with their corresponding flowering seasonality and flower colours is given in Tables S1–S3 (see Supplementary Material online). The invasive and randomly selected plant species were categorized based on their flowering seasonality and flower colour polymorphism into multi-seasonal flowering with flower colour polymorphism (MP), multi-seasonal flowering with single flower colour (MS), seasonal flowering with flower colour polymorphism (SP), and seasonal flowering with single colour (SS).

The results of our analysis show that the percentage of plant species in MP and MS is comparatively higher in invasives than the random set of plant species. Percentage of plant species in SP and SS categories is higher in random sets of plant species when compared to invasive species (Figure 1). Statistical analysis revealed that the invasive species showed significant difference ($P < 0.001$) in the traits of MP, SP and SS categories when compared with both sets (regional and global levels) of randomly selected plants. Multi-seasonal flowering with single flower colour showed no significant difference in phenological trait for both comparisons (invasive with regional level random; $P = 0.057$ and invasive with global level random; $P = 0.188$). The overall analysis of phenological behaviour revealed that the invasive species differed significantly ($P < 0.001$) from both the randomly selected sets of species (Tables 1 and 2). In the regional level randomly selected dataset, the percentage of species which possessed seasonal flowering (57) and single flower colour (58) was found to be maximum. In randomly selected global dataset, the percentage of species which displayed seasonal flowering (63) and single flower colour (72) was found to be maximum. Invasive plant species data revealed that 94% of the species were multi-seasonal in flowering and 62% of the species exhibited flower colour polymorphism (Figure 2). A binary logistic regression analysis was performed to predict the odds of invasion in relation to various categories of phenological traits such as MP, MS, SP and SS categories in a sample space including all the 858 non-repetitive species. The SS category was considered as the base category. A test of the full model was statistically significant ($\chi^2 = 278.73$, d$f = 3$, $P < 0.001$) and overall prediction success of the model was 76.2%. The Wald criterion demonstrated that MP and MS categories made significant contribution to the prediction ($P = <0.001$ in both cases). The logit value [exp(B) value] showed that the odds ratio was 50.25 times higher for MP category and 20.22 times higher for MS category in relation to the base SS category.

Loss of function mutations in flower colour genes and selection imposed by non-pollinating agents on the pleiotropic effects of these genes produce flower colour morphs in plant species[10]. Natural selection maintains more than one colour morph of a given species by means of fluctuating[11–13], stabilizing and balancing[14,15] and negative frequency-dependent[15–17] types of selection. The flower colour morphic species as invasives can exploit a variety of pollination systems leading to differential pollination success among the colour morphs of a species. This assumption has been supported by either differential pollinator visitation to different colour morphs[14,16,18–21], or preferential visits by pollinators to specific colour morphs[17,22–25] in flower colour morphic species. Flower colour morphic

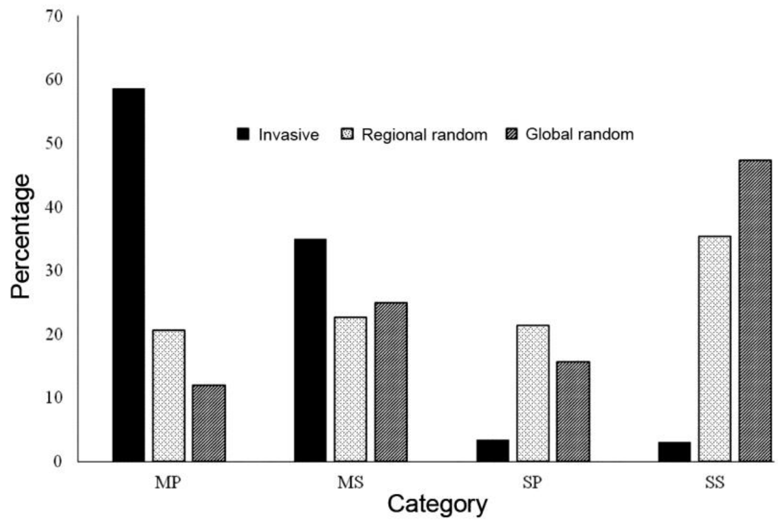

Figure 1. Percentage of plants with multi-seasonal flowering with flower colour polymorphism (MP), multi-seasonal flowering with single flower colour (MS), seasonal flowering with flower colour polymorphism (SP), and seasonal flowering with single flower colour (SS) of invasive, randomly selected regional-level[8] and randomly selected global-level[9] plant species.

Table 1. Chi-square analysis between invasive and randomly selected regional-level plant species[8] under different phenological categories

Category	No. of plants		χ^2	d*f*	*P*-value
	Invasive (*n* = 263)	From regional flora (*n* = 300)			
Multi-seasonal flowering with flower polymorphism (MP)	154	062	39.185	1	<0.001
Multi-seasonal flowering with single flower morph (MS)	092	068	3.600	1	0.057
Seasonal flowering with flower polymorphism (SP)	009	064	41.438	1	<0.001
Seasonal flowering with single flower morph (SS)	008	106	84.246	1	<0.001
All phenological categories	–	–	166.760	3	<0.001

Table 2. Chi-square analysis between invasive and randomly selected global-level plant species[9] under different phenological categories

Category	No. of plants		χ^2	d*f*	*P*-value
	Invasive (*n* = 263)	From regional flora (*n* = 300)			
MP	154	036	73.284	1	<0.001
MS	092	075	1.7305	1	0.188
SP	009	047	25.786	1	<0.001
SS	008	142	119.710	1	<0.001
All phenological categories	–	–	219.020	3	<0.001

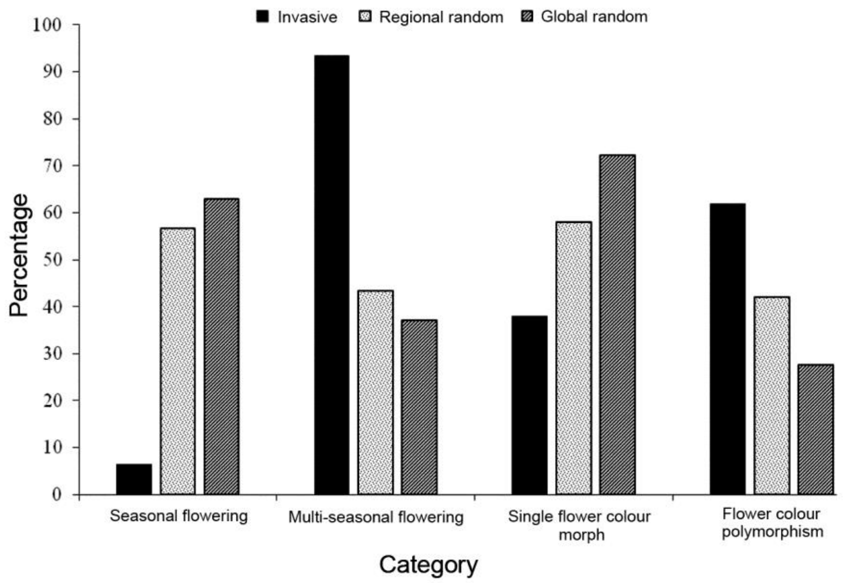

Figure 2. Percentage incidence of plant species within different categories of invasive, randomly selected regional-level[8] and randomly selected global-level[9] plant species.

species may also exploit pollinator shift of native species in invaded regions[19]. Recent studies have shown that invasive species have become well integrated into the native pollinator networks. Such an ability of integration would be relatively high in flower colour morphic species with two or more colour morphs. One might infer from the above that the invasive species have a competitive advantage over the native species. Thus, invasive plant species which also possess flower colour polymorphism and multi-seasonal flowering have a collective advantage over native species by attracting diverse range of pollinators as well as seed production through the year.

The pleiotropic effects of flower colour genes play a role in deciding the plant fitness traits in flower colour morphic species. Evidences have clearly shown that flower colour morphs vary among them in such traits, particularly reproductive traits[16,18–20,22,26–31]. Quantitative evidences for such variable fitness traits in flower colour morphic species are given in Strauss and Whittall[30]. The production of herbivore defence chemicals as well as floral colour pigments is rooted in the anthocyanins biosynthetic pathway and its branches. Studies have shown that allelochemicals present in the plants influence preference and performance of herbivores in plants[31,32]. Flower colour polymorphs show variations in the production of such chemicals, qualitatively as well as quantitatively[31–35]. More remarkably, pollinator preference, herbivore damage and flower colour are three components linked together in many species[24,36–40]. According to the available data[31,41], at least one colour morph with considerable chemical defence might escape and succeed at the invaded zones. Recent literature on the phenological behaviour of invasive plants shows that they can attract a wide range of pollinators by producing more floral rewards[42–44], escaping herbivore damage[31,32] and possess greater reproductive fitness[45] than natives.

In conclusion, our assumptions on the role of pollinator preference, herbivore defence and reproductive fitness traits on the invasive potential of flower colour morphic and multi-seasonal species are interlaced substantially with the major existing hypothesis on plant bioinvasion. Further collective research on the plant reproductive fitness traits, plant–pollinator interactions and herbivore defence in different colour morphs of invasive plants will strengthen this hypothesis in future. The phenological characteristics such as flower colour polymorphism and multi-seasonal flowering can be used as markers to identify potential invasive species.

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