SPATIAL VARIATION IN POLLINATOR COMMUNITIES AND REPRODUCTIVE PERFORMANCE OF *PROSOPIS JULIFLORA* (FABACEAE)

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Abstract— This study was conducted in an effort to understand the effects of spatial variations in pollinator assemblage due to habitat isolation on the reproductive performance of perennial plant species. Variations in pollinator assemblage structure (abundance, diversity and Shannon-Wiener index) were studied at three widely isolated (100 to 200 km apart) nature reserves of Southern Punjab, Pakistan, in order to explore its effects on reproductive performance of *Prosopis juliflora.* Species richness and abundance were highest in Pirowal Sanctuary followed by Chichawatni Sanctuary and Chak Katora forest reserve. The pollination system of *P. juliflora* was highly generalized with 77 insect visitor species in four orders among all the three sites. However, pollinator assemblage varied significantly in composition among the sites. Out of the four reproductive parameters considered, the number of pods per raceme and germination varied significantly among the three locations. The reproductive performance of *P. juliflora* in terms of number of pods per raceme and germination improved with abundance of pollinators.

Keywords: pollinator assemblages, Prosopis juliflora, *reproductive success, spatial variation*

INTRODUCTION

Pollinator assemblage structure can have important influences on floral evolution and reproductive interactions among plant species (Moeller 2005). Recent studies of structure of plant-pollinator networks have shown that they exhibit 'nestedness', i.e. specialist pollinators and plants are subsets of more generalised networks (Kallimanis et al. 2009). Following these ideas, an increasing number of community-level studies have concluded that generalization is the rule and specialization is rare (e.g., Olesen & Jordano 2002). However, most studies have not distinguished between pollinators and floral visitors, despite the fact that a visitor may not actually pollinate the flowers.

Pollination systems can be examined in the same general framework used to understand community structure and assembly. For example, the variation of visitor abundance and their spatial predictability within plant populations allow regular floral visitors to be distinguished from occasional or incidental floral visitors (Root 1973). From the ecological point of view, generalization is considered a positive trait that may favour competitive ability, colonization capacity and invasion ability in plants (Richardson et al. 2000).

In a geographical context, the spatial structure of variation in pollinator abundance and community composition can also have important implications for plant reproductive performance and ultimately floral evolution (Gomez et al. 2007). This spatial scale variation in pollinator communities remains poorly documented. Flower visitation activity of pollinators is often strongly affected by climatic conditions (McCall & Primack 1992) and climate varies on both large and small spatial scales. The size and quality (availability of nesting places and floral resources) of any natural habitat also determines the richness and abundance of pollinator species (Cunningham 2000).

When large tracts of forests are subjected to fragmentation due to deforestation, the organisms remaining in discontinuous remnants are exposed to many biotic and abiotic changes (Saunders et al. 1991). The survival of any species under such conditions depends on its life history, ecological characteristics and mutualistic interactions (Rathcke & Jules 1993). Habitat isolation and quality certainly affects pollinator diversity and hence reproductive success of plants, but seed set may also be influenced by other factors such as patch size, density of flowering plants, occurrence of competing alternative flowers (Jennersten & Nilsson, 1993; Kleijn & Langevelde 2006), genetic variability (Van Treuren et al. 1994) and abundance of pollinators (Donaldson et al. 2002).

Previously, many studies assessed the affect of habitat quality and fragmentation or isolation on the diversity and abundance of pollinators and ultimately plant reproductive success (Steffan-Dewenter & Tscharntke 1999; Donaldson et al. 2002; Murren 2002). These studies were done on small scales, i.e. either on islands or in isolated patches of forest in single habitats suffering from deforestation. Our study was conducted on a different scale: The study locations in this research were relatively large (> 1000 acres) and widely separated (100 - 200 km) from each other. Since there is no geographical barrier in the plains of Punjab, we can presume that thousands of years back, the entire study area may have been covered by continuous, similar vegetation and inhabited by a homogenous population of pollinator species. However, the distribution of pollinators may vary in

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space and time (Ollerton & Cranmer 2002). Very few studies have explicitly tested for spatial variation in pollinator richness and diversity (Herrera 2005).

This study focuses on the invasive *Prosopis juliflora* (Sw.) DC, a multipurpose perennial tree native to northern South America. Its fast growth, drought resistance and salt tolerance has led to its successful naturalization in dry tropical and sub-tropical areas of Africa, south-east Asia, the Indian sub-continent and Australia. It was deliberately introduced to the sub-continent in 1857 (Luna 1996) with view point of its qualities and uses, i.e. construction material, charcoal, soil conservation and rehabilitation of degraded and saline soils (Pasiecznik et al. 2001). Due to improper management, however, its potential benefits were undermined, because it becomes a serious invasive tree (Pasiecznik 2001). Its invasive qualities have resulted in multiple negative effects on food security, livelihoods and environment in many parts of the world, e.g. Ethopia (Dubale, 2006), India and Kenya (Mwangi & Swallow 2005) by declining livestock production and productivity due to its competition with palatable native trees.

P. juliflora is self-incompatible (Simpson 1977) and receives visitors from a variety of insect orders (Ward et al. 1977). Many pollination biologists have explored the reproductive biology of *P. juliflora* (DeOliveira & Pires 1990; Iqbal & Shafiq 1997; Zaitoun et al. 2009). About 300-400 flowers are arranged on a raceme (Zaitoun et al. 2009). An individual flower has petals only 3 mm wide while its anthers are 4 mm wide. The small size of the flower ensures contact of even small insect with reproductive organs and minimizes the risks of nectar robbing. Thus, it is fair to assume that all species recorded act as effective pollinators to some degree.

We investigated *P. juliflora* populations in three widely separated wildlife reserves (*ca.* 100 to 200 km apart from each other) of the southern Punjab (Pakistan). The aim was to study (i) variation in the pollinator community structure (species richness, diversity and abundance) among these reserves due to their isolation a hundred years ago; and (ii), whether the variation in pollinator community structure affects the reproductive performance of *P. juliflora*.

MATERIALS AND METHODS

Study area

The study was conducted in the southern Punjab of Pakistan. Climate of the area is sub-tropical with cold winter and hot summer; the mean monthly temperature ranges between 25°C and 30°C, with mean maxima 35°C to 40°C, and mean minima 10°C to 20°C. The extreme maximum temperature of the region varies between 45°C and 48°C, recorded in May and June, while the lowest minimum temperature is 0°C to -2°C, recorded in January. May and June are the hottest months, whereas January is the coldest month of the region (Khan et al. 2010). We selected three natural habitats: Chichawatni Sanctuary (District Sahiwal), Pirowal Sanctuary (District Khanewal) and Chak Katora forest reserve (District Bahawalpur) (Table 1). Chichawatni is 100 km north-east from Pirowal, while Chak Katora is 150 km south-east: between them are either cities or agricultural land. These natural habitats have never been cultivated and according to the definition as wildlife sanctuary, entry is prohibited without official permission. The largest (17 823 acres) is Pirowal, where we selected a fenced area of 1500 acres with very few human activities (wood cutting only). Chichawatni is smaller (11 530 acres) with low level human interventions like grazing and wood cutting, while Chak Katora is the smallest fragment (only 1 323 acres) with more grazing and wood cutting than the other two locations.

Flower visitor census

Flowering of *P. juliflora* and our study took place during the hottest season from April to June in 2008. In each location we chose four experimental plots (*ca.* 2 acres each) with similar population size (*ca.* 100 trees) of *P. juliflora* and selected 25 similar sized trees in each plot, widely separated from each other. On each tree, we tagged one branch ~10ft long originating from the main stem. Once at every fortnight, from first week of April to end of June, the number of individuals of each insect species visiting the flowers on these tagged branches was counted for 60 seconds/branch. We reselected another branch on the same tree if the chosen one was not flowering. Records were taken on sunny days from 08:00 to 11:00 h (local time). This fortnightly data were completed on three consecutive days (one day per site).

All the visitors were morphotyped and counted in free flight, while later identification was done in the laboratory. Identification of Diptera and Coleoptera was accomplished by using standard keys (Borror et al. 1981). Syrphids (Diptera: Syrphidae) and butterflies (Lepidoptera:

TABLE 1. Properties and types of three studied nature reserves at southern Punjab, Pakistan.

Location	Type of reserve	Area (acres)	GPS	Altitude (feet)	Human intervention
Pirowal District Khabewal	Wildlife Sanctuary (fenced)	17 823	30°34′ N 72°03′ E	437±16.5	Very low (wood cutting)
Chichawatni District Sahiwal	Wildlife Sanctuary (unfenced)	115 30	30°54′ N 72°70′ E	205±22	Low (Grazing and wood cutting)
Chak Katora District Bahawalpur	Reserve forest (unfenced)	1 323	29°78′ N 72°55′ E	447±19.4	Intensive (Grazing and wood cutting)

Rhopalocera) were identified to species by experts (see Acknowledgement). The keys of Michener (2000) were used to identify bee genera. The voucher specimens were deposited at the Agricultural Museum of the University College of Agriculture, Bahauddin Zakariya University Multan.

Reproductive success

Since the pod-setting percentage is very low in *P. juliflora* (De Oliveira & Pires 1990), we tagged three branches on each of the 25 sampled trees in each location and harvested all the mature pods fortnightly. Plant reproductive success was measured in terms of number of pods per raceme, pod length, 100-seed weight, number of seeds per pod and percentage germination. Seeds were mixed thoroughly and 500 seeds were randomly selected and subjected to germination test in plastic pots for each location.

Data analysis

Two traits of the flower visitor assemblage visiting *P. juliflora* flowers are analyzed in this study, i.e. abundance (total number of flower visits) and diversity (Magurran 2004). We assessed flower visitor diversity by calculating species richness, diversity, evenness and dominance. Species richness is simply the number of insect visitor species in each location. Dominance was calculated as the relative abundance of the most abundant visitor species. We used pollinator rank-abundance plots as a way to visualize the structure of the pollinator communities (Magurran 2004). Diversity was calculated using Shannon-Wiener index and Hurlbert's Probability of an Interspecific Encounter (PIE) index (Hurlbert 1971). Hurlbert's PIE is an evenness index that combines the two mechanistic factors affecting diversity, i.e. dominance and species abundance which itself is the complement of Simpson's index.

Among-location differences in pollinator abundance, richness, diversity (Shannon-Wiener and Hurlbert indices) and plant reproductive success were analyzed with one-way ANOVA, followed by the multiple-comparison Least Significant Difference (LSD) test. Richness, dominance and diversity (Shannon-Wiener and Hurlbert indices) were compared among the locations using individual-based rarefaction curves generated by EcoSim (Gotelli & Entsminger 2005); the graph was drawn in PAST software (Hammer et al. 2001). Rarefaction allows for estimation of number of species (S) expected in a random samples of N individuals taken from a larger collection made up of N individuals and S species (Gotelli & Entsminger 2005).

The effect of pollinator diversity on plant reproductive success was explored with simple linear regression analysis between species richness, abundance and Shannon-Wiener index as predictors and components of reproductive success as responses.

RESULTS

A total of 800 insects belonging to 77 species in four orders were observed visiting the flowers of *P. juliflora* in the three isolated locations. The majority of species were Hymenoptera (41) and Diptera (17; Fig. 1). Only four species made up more than 6% of the total visits across all sites. These species were two long-tongued large bees (*Apis dorsata* and *A. florea*) and two syrphid flies (*Eristalinus aeneus* and *Ischiodon scutellaris*). Considering the seven most abundant floral visitors across all sites (Fig. 2), four species (*A. florea*, *A. dorsata*, *Megachile* sp. and *E. aeneus*) had long mouth parts (3.44, 6.14, 5.22 and 4 mm, respectively; Somanathan et al. 2009; Chaiyawong et al. 2004) and three species (*I. scutellaris*, *Episyrphus balteatus* and *Agapostemon* sp.) had shorter mouth parts (2-3 mm; Gilbert, 1981). Among these four most abundant floral visitors, *E. balteatus* and *A. dorsata* were the most abundant at Chichawatni (Appendix 1) while *E. aeneus*, *I. scutellaris* and *A. florea* at Khanewal. On the other hand, *E. aeneus* and *I. scutellaris* were not observed in Chak Katora, which was dominated by two bees *Megachile* sp. 2 and *Agapostemon* sp.

Pollinator assemblage structure was similar in three locations with few abundant species and high number of scarce species (Fig. 2), but the assemblage varied significantly in composition among the sites. The most abundant species in three locations also varied (Fig. 2). Eleven species (two fly, two bee, three wasp, two butterfly and two beetle species) were observed solely in Chichawatni (Appendix 1). Five species (one dipteran, one wasp, two butterfly and one beetle species) were restricted to Chak Katora while seventeen species (two flies, ten bees, three wasps, one butterflies and one moth) occurred only in Khanewal. Twelve species were commonly found in the three locations, i.e. four fly, four bee, one wasp and three butterfly species (Appendix 1).

At all three sites Hymenoptera was the largest order in terms of abundance and number of species followed by Diptera (Fig. 1). There was significant variation in pollinator abundance among sites in terms of visitation frequency ($F = 0.037$, $df = 126$, $P = 0.05$). The maximum visitation frequency (5.22 individuals per 30 minutes) was observed in Pirowal followed by Chichawatni and Chak-Katora (3.50 and 1.59 individuals per 30 minutes).

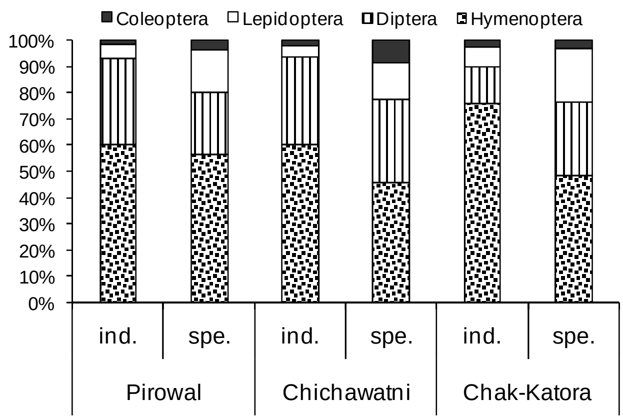

FIGURE 1. Percentage of species (spe.) and individuals (ind.) of related insect orders visiting *Prosopis juliflora* flowers at three locations in southern Punjab during 2008.

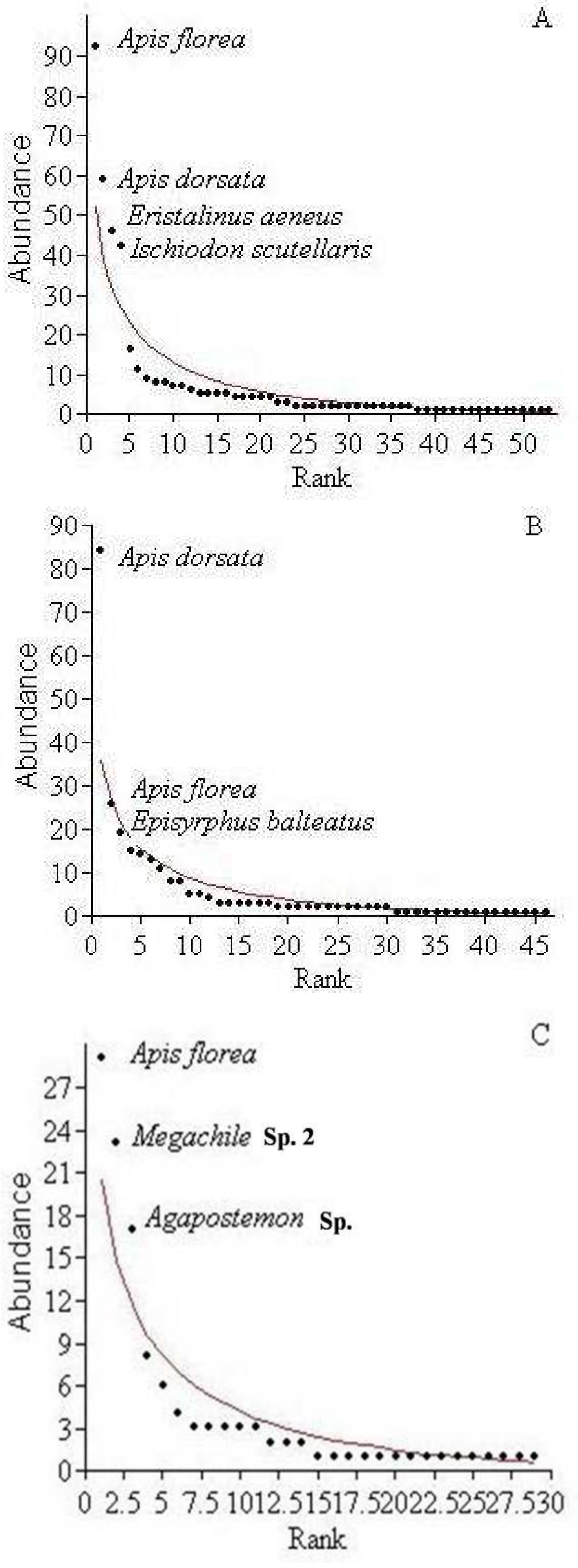

FIGURE 2. Rank-abundance (total numbers over complete study period) curves of insect species visiting flowers of Prosopis juliflora at three locations (A: Pirowal; B: Chichawatni; C: Chak-Katora) in Southern Punjab. The names of the species accounting for at least 10% of the visits at a given location are provided.

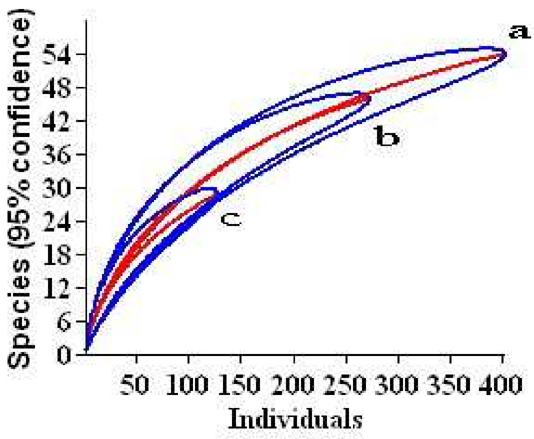

FIGURE 3. Rarefaction curves of three locations, i.e. (a) Pirowal (b) Chichawatni (c) Chak-Katora, based on individual rarefaction method showing the expected number of species as a function of sample size.

The rarefaction curves of three locations based on individual rarefaction method (using the expected number of species as a function of sample size) have not yet reached an asymptotic level so species richness can be expected to increase with sampling effort (Fig. 3). There was a significant difference ($F = 35.79$, df = 82.18, $P = 0.00$) in species richness among the three locations (Table 2) i.e. highest in Pirowal followed by Chichawatni and Chak-Katora. One-way ANOVAs showed that there were no significant differences in seeds per pod and seed weight of *P. juliflora* among the three sites, but there were significant differences in the number of pods per raceme and germination. Significantly more pods per raceme were recorded in Chichawatni and Pirowal than Chak-Katora ($F = 70.33$, df = 75, $P < 0.001$), whereas germination percentage showed a non-significant (df = 27, $F = 2.35$, $P = 0.114$) tendency being higher in Pirowal (51%) than Chichawatni (41.2) and Chak-Katora (40.8%). The number of pods per raceme and germination appeared pollinator limited (Table 3).

Since there were no significant differences in seeds per pod and seed weight among the three locations, we did not relate them to species abundance, richness and Shannon-Wiener index. Only significantly varying components were selected for that purpose, i.e. number of pods per raceme and germination. Abundance was positively related to the number of pods per flower and germination. Species richness and the Shannon-Wiener index (Fig. 4) were not related.

DISCUSSION

The pollination system of *P. juliflora* is extremely generalized. Its brush-shaped flowers were visited by 77 insect species with different morphology, size and behaviour from a variety of functional groups, i.e. short-and long-tongued bees, butterflies, flies and beetles. Previous studies

TABLE 2. Among-location differences in pollinator abundance and diversity.

Locations	Abundance	Dominance	Shannon-Wiener	Species Richness	Hulbert
Pirowal	5.22 a	0.24 b	2.68 a	36.42 a	0.88 a
Chichawatni	3.50 ab	0.32 a	2.58 a	30.35 b	0.87 a
Chak-Katora	1.59 b	0.27 ab	2.31 b	18.95 c	0.89 a

TABLE 3. Comparison of reproductive success of three locations.

	No of pods/raceme	No of seed/pod	100-Seed weight (gm)	Germination (%)
Pirowal	5.829 a	10.77 a	2.767 a	51.00 a
Chichawatni	6.413 a	10.95 a	2.778 a	41.20 b
Chak-Katora	3.241 b	10.90 a	2.787 a	40.80 b

Mean values sharing similar letters in respective columns show non-significant differences ($P < 0.05$) after LSD test.

have also failed to relate any particular functional group of insects to the evolution of brush-shaped flowers (Hingston & McQuillan 2000; Devy & Davidar 2003). Given the morphology of *P. juliflora* flowers, contact of insect visitors with flower's reproductive organs is unavoidable. Muzaffar and Ahmad (1991) noted *P. juliflora* as a major nectar and pollen resource for bees in Pakistan.

Prosopis juliflora is not native to the sub-continent, yet it received visits by a large array of potentially pollinating insects. Pollination success in *P. juliflora* is always low and very few legumes are produced despite large numbers of flowers per tree: DeOliveira & Pires (1990) reported a pollination efficiency of 29% in *P. juliflora* based on the number of inflorescences per tree. However, when related to the number of flowers, it dropped to 1.48%

The low fruiting success under open pollination as well as under exclusion of pollinators indicates that *P. juliflora* is more or less incapable of autonomous selfing (DeOliveira & Pires 1990). Another reason could be that many plant species mass-flower to increase floral display and abort most of their flowers and may not have enough resources to develop fruits from all these flowers (Trueman & Wallace 1999). The total number of seeds produced by one individual may, however, still be high enough for the species to survive (Karron & Mitchell 2011). Several reasons have been documented for the low reproductive success by DeOliveira & Pires (1990): poor pollen viability, short period of pollen release or stigma receptivity, lack of synchronization between pollen release and pollen reception, flower sterility or high rates of ovary abortion, few pollinating insects at the time of maximum receptivity. Goel & Behl (1995) found maximum pollen production in *P. juliflora* at midday, but insects are less mobile during high temperatures at this time (ca 40°C in this study).

The pollinator assemblage in rank-abundance curves revealed *A. dorsata* and *A. florea* as the most abundant species in all three locations. A single colony of *Apis* may have thousands of workers and trees provide ideal nesting locations, making them the most dominant visitors, as in case of this study. Both species have already been reported as the most dominant floral visitors of various crops (Sajjad et al. 2008; Sajjad et al. 2009; Ali et al. 2011) in the study location.

We also found a significant spatial variation among locations in pollinator assemblages in terms of species richness, diversity and dominance. The abundance-richness relationship is frequent in pollinator assemblages (Steffan-Dewenter et al. 2002), i.e. few abundant species and high number of scarce species in this study. The observed species richness ranged from 19 to 34 species. The highest species richness was recorded in the largest and least disturbed site, at Pirowal. Habitat quality includes factors that directly influence the life history of a pollinator species, i.e. availability of breeding and shelter places and host plants (Winfree et al. 2011). The surrounding quantity and quality of habitats is usually positively related to insect species richness and abundance (Oeckinger & Smith. 2007) but the discovery of these relationships may depend upon the scale of investigation.

Perennial plant species respond in different ways towards habitat fragmentation and it is difficult to find a clear rule in general (Donaldson et al. 2002), i.e. populations in small fragments do not always experience pollination deficits. However, many other studies suggest a better plant reproductive performance in larger reserves or mainland than smaller ones or on islands (Jennersten 1988; Cunningham 2000; Donaldson et al. 2002; Murren 2002).

Our data clearly suggests that for *P. juliflora,* the number of pods and germination rate of seeds rise with abundance of its flower visitors. Further, flower visitor abundance was a better predictor of plant reproductive performance than species richness and the Shannon-Wiener index. This might be because of less sensitivity of Shannon-Wiener index to actual site differences, i.e. the Shannon-Wiener index can be similar even if two sites are different in species richness. Only few studies give empirical evidence regarding consequences of pollinator assemblage on plant reproductive success concerning pollen limitation. Diversity and identity (Gomez et al. 2010), and relative abundance of floral visitors (Sahli and Conner 2006) have been reported as the important predictors of plant reproductive success. The sensitivity of pollinator assemblages to predict plant reproductive success

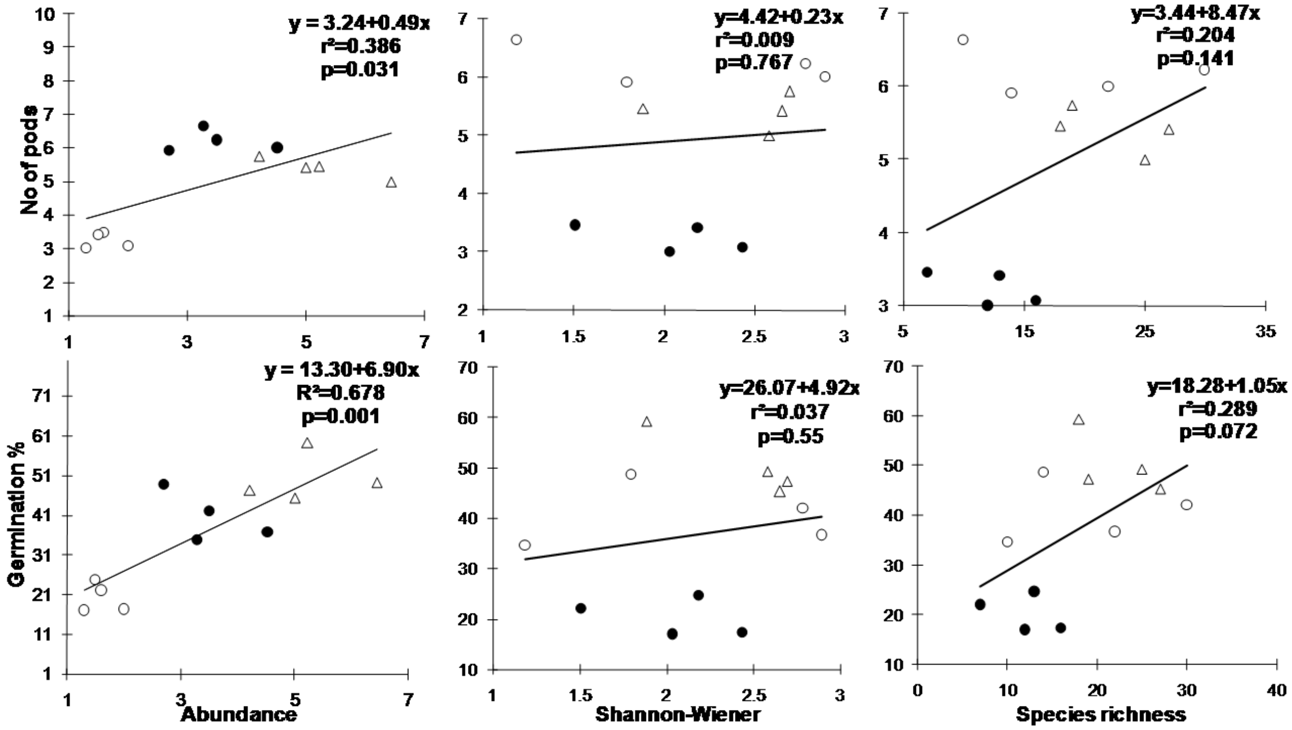

FIGURE 4. Relationship between flower visitor abundance, species richness and diversity (Shannon-Wiener) and plant reproductive performance measured as germination % (lower graphs) and fructification (number of pods, upper graphs) in *P. juliflora* at southern Punjab, Pakistan. Open triangles: Pirowal; Open circles: Chichawatni; Solid circles: Chak-Katora.

may vary with plant species and the pollination effectiveness of available pollinator species (Talavera et al. 2001).

In conclusion, flower visitor spectra of *P. juliflora* at Pirowal and Chichawatni were more species rich and abundant than at Chak-Katora possibly due to the former two sites being larger and least disturbed if not undisturbed compared to the latter. This ultimately affected insect visitation frequency and hence fruit set of *P. juliflora*. In contrast to flower visitor abundance, species richness and the Shannon-Wiener index were no good predictors of reproductive performance of *P. juliflora*.

APPENDIX

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

APPENDIX I. Insects visiting *P. juliflora* from April to June 2008 in three selected locations.

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