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POLLINATION ECOLOGY OF THE INVASIVE TREE TOBACCO *NICOTIANA GLAUCA*: COMPARISONS ACROSS NATIVE AND NON-NATIVE RANGES

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Abstract—Interactions with pollinators are thought to play a significant role in determining whether plant species become invasive, and ecologically generalised species are predicted to be more likely to invade than more specialised species. Using published and unpublished data we assessed the floral biology and pollination ecology of the South American native *Nicotiana glauca* (Solanaceae) which has become a significant invasive of semi-arid parts of the world. In regions where specialised bird pollinators are available, for example hummingbirds in California and sunbirds in South Africa and Israel, *N. glauca* interacts with these local pollinators and sets seed by both out-crossing and selfing. In areas where there are no such birds, such as the Canary Islands and Greece, abundant viable seed is set by selfing, facilitated by the shorter stigma-anther distance compared to plants in native populations. Surprisingly, in these areas without pollinating birds, the considerable nectar resources are only rarely exploited by other flower visitors such as bees or butterflies, either legitimately or by nectar robbing. We conclude that *Nicotiana glauca* is a successful invasive species outside of its native range, despite its functionally specialised hummingbird pollination system, because it has evolved to become more frequently self pollinating in areas where it is introduced. Its invasion success is not predictable from what is known of its interactions with pollinators in its home range.

Key words: Argentina, California, Canary Islands, Greece, hummingbird, invasive species, Israel, mutualism, Peru, pollination, Solanaceae, South Africa, sunbird

INTRODUCTION

Plant-flower visitor relationships evolve and are maintained within a fluctuating ecological context in which populations of pollinating, pollen collecting and nectar robbing animals can change significantly from year to year (e.g. Herrera 1988; Fishbein & Venable 1996; Ollerton 1996; Lamborn & Ollerton 2000; Alarcón et al. 2008). This is particularly relevant to introduced invasive plant species which lack ecological or functional pollinator specificity and are therefore ecological generalists (*sensu* Waser et al. 1996; Fenster et al. 2004; Ollerton et al. 2007). Such plants can form relationships with pollinators and maintain viable populations following human dispersal beyond their native range, negatively affecting local habitats by monopolising space and soil resources, and in the process out-competing native species (Theoharides & Dukes 2007).

Invasive plants have also been shown to have more subtle, but still potentially important, detrimental effects on the native flora by becoming integrated into local pollination interaction webs (*sensu* Memmott & Waser 2002; Vilá et al. 2009; Padrón et al. 2009) and influencing patterns of flower visitation and pollen flow, resulting in lower seed set and quality, and reduced pollinator abundance (Chittka & Schürkens 2001; Schürkens & Chittka 2001; Moragues & Traveset 2005; Traveset & Richardson 2006; Bjerknes et al. 2007; Aizen et al. 2008; Morales & Traveset 2009; Stout & Morales 2009). Other studies, however, have found no negative effects (e.g. Aigner 2004) indicating that the outcomes of such indirect interactions are likely to be species and/or community specific (Moragues & Traveset

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2005) and also to depend on intensity of invasion (Dietzsch et al. 2011) and spatial scale (Cariveau & Norton 2009). It is therefore important for us to understand why some plant species are more likely than others to become a threat to local plants, and particularly whether such plants can be predicted from their floral traits (Rodger et al. 2010, though see the recent exchange of views in Trends in Ecology and Evolution stimulated by Thompson & Davis 2011). For example, Chittka & Schürkens' (2001) study suggests that introduced plants with very high rates of nectar production may draw pollinators away from native plants, reducing their reproductive success. High rates of nectar production may therefore be a predictive trait for such negative indirect effects (although see Nienhuis et al. 2009).

Other than self-pollinating species, plants with ecologically generalized pollination systems, which can attract, reward and therefore utilise a wide range of pollinators, have been considered the most probable invasive species (Baker 1974; Richardson et al. 2000; Olesen et al. 2002; Vilá et al. 2009). Such plants are theoretically more likely to co-opt native or introduced flower visitors as pollinators, ensuring their reproductive success and subsequent invasiveness, and there is growing evidence that this is the case (e.g. Forster 1994; Stout 2007; Bartomeus et al. 2008; Vilá et al. 2009; Harmon-Threatt et al. 2009). Nevertheless more studies are required to test the generality of this idea. In particular we should compare the pollination ecologies of invasive plants within their normal distributional range and within the areas of invasion. The only such published study that we know to exist is of *Rhododendron ponticum* (Stout et al. 2006, though see Rodger et al. 2010) and this is a gap in the knowledge of the ecology of invasive species generally (Tillberg et al. 2007).

This paper focuses on the invasive tree tobacco *Nicotiana glauca* Graham (Solanaceae), a native of central and north west Argentina and Bolivia (Goodspeed 1954) which has been widely introduced to the subtropics as a garden ornamental, only to escape and densely colonise native habitats across the globe, including other parts of South America (Moraes et al. 2009; Cocucci, Watts, pers obs.); Australia (Florentine & Westbrook 2005; Florentine et al 2006); California (Schueller 2004); Hawaii (Izhaki, pers. obs.); the north and east Mediterranean region (Tadmor-Melamed et al. 2004, Bogdanović et al. 2006) including Israel where *N. glauca* was first observed in 1890 (Bornmuller 1898); Mexico (Hernández, 1981); North Africa (Ollerton., pers. obs.); Southern Africa (Geerts & Pauw 2009; Henderson 1991; R. Raguso, pers comm.); and the Canary Islands (Kunkel 1976; Ollerton pers. obs.; Stout pers. obs.). The species is listed in the Global Invasive Species Database (http://www.issg.org/ase/welcome/), and a number of regional organisations consider it invasive, for example in Hawai'i (http://www.hear.org/pier/species/nicotiana_glauca.htm), Europe (http://www.europe-aliens.org/index.jsp) and South Africa (http://www.agis.agric.za).

In its native range, *N. glauca* is strictly hummingbird pollinated (Nattero & Cocucci 2007) although bees and other insects may pierce the base of the corolla tube to rob nectar. Our study therefore addresses the following two questions:

(1) Is *N. glauca*, with its apparently functionally specialised pollination system and abundant nectar resources, pollinated by functionally equivalent pollinators (i.e. flower-feeding birds) throughout its native and non-native range?

(2) Are these interactions with local pollinators (i.e. integration into the local pollination web) a prerequisite for reproductive success in this highly invasive species?

DATA COLLECTION AND SYNTHESIS

We have synthesised published and unpublished data from studies of the species in north western Argentina and Bolivia (Nattero & Cocucci 2007, Nattero et al. 2010, and unpublished data), where the species is native, with research from areas where the species is introduced, including South America (Peru – Watts unpublished data); other populations of Argentina outside the native range (Nattero & Cocucci 2007 and unpublished data); North America (México – Hernández 1981; California – Schueller 2004 and 2007 and unpublished data); and the Old World, including Tenerife (Ollerton et al. unpublished data), Gran Canaria (Stout unpublished data), Greece (Schueller 2002 and unpublished data) and Crete (Ollerton unpublished data); Israel (Tadmor-Melamed 2004; Tadmor-Melamed et al. 2004; Izhaki unpublished data); and South Africa (Skead 1967; Knuth 1898-1905; Marloth 1901; Geerts & Pauw 2009 and unpublished data).

The methods for the published data collection can be found in the relevant papers; methods for the unpublished data are summarised only briefly and more details can be obtained via the corresponding author. Measurements of floral traits, including nectar production, followed standard protocols (Kearns & Inouye 1993; Dafni et al. 2005). Unless otherwise stated, the authors cited above were responsible for the data collected in specific geographical regions. Data were analysed using SPSS 17.0: all data fulfilled assumptions of normality (one-sample Kolmogorov-Smirnov Test) and mean values are presented as ± SD unless otherwise stated.

DISTRIBUTION, REPRODUCTION AND ABUNDANCE OF *NICOTIANA GLAUCA*

Within its native range *N. glauca* is an occasional plant of dry, naturally and anthropogenically disturbed areas such as river banks, track sides and abandoned quarries. It is found mainly in semi-arid environments from low to high altitudes (0-3500 m), but never at wet localities. The plant is rarely abundant and is mainly found as scattered, usually multi-stemmed individuals, though stem densities on anthropogenically disturbed sites can range from 3.0 to 12.5 m^{-2} (Nattero & Cocucci 2007). Mean population fruit set per plant ranges from about 28.0% to 67.0% (grand mean = 42.4 ± 13.1% - Table 1).

TABLE 1: Reproductive output and mean stigma-anther distances of populations of *Nicotiana glauca*. Stigma-anther distances were measured to the nearest 0.1 mm using a digital calliper. Sample sizes vary considerably and are available from the corresponding author on request. All means are ± SD. Status: N = Native, I = Introduced

Region	Locality	Status	Mean fruit set (%)	Mean minimum stigma-anther distance (mm)
Argentina and Bolivia (Nattero and Cocucci 2007, Nattero et al. unpublished data)	Tupiza	N	36 ± 25	2.2 ± 0.8
	Cuesta de Miranda	N	39 ± 16	1.2 ± 0.6
	Cochabamba	N	32 ± 14	3.0 ± 0.8
	Dique Los Sauces	N	28 ± 17	2.6 ± 0.8
	Potosí	N	47 ± 10	3.6 ± 1.1
	Sanagasta	N	48 ± 26	1.3 ± 0.8
	Sucre	N	67 ± 16	2.6 ± 1.5
	Paraná	I	67 ± 7	2.5 ± 0.9
	Costa Azul	I	41 ± 18	1.2 ± 0.6
	Bella Vista	I	56 ± 8	1.2 ± 0.8
Peru (Watts, unpublished data)	Urubamba	I	-	1.7 ± 0.4
California (Schueller 2004)	Santa Cruz Island	I	41 ± 49	1.6 ± 0.3
	Santa Catalina Island	I	75 ± 20	1.8 ± 0.2
	Sedgwick Reserve	I	26 ± 44	1.9 ± 0.5
	Starr Ranch	I	70 ± 46	2.1 ± 0.2
Israel (Izhaki, unpublished data)	Jezreel Valley	I	55 ± 8	1.8 ± 0.7
Tenerife (Ollerton et al., unpublished data)	South West	I	80 ± 21	1.4 ± 0.4
Greece (Schueller, 2002 and unpublished data)	Athens (Ano Illioupolis)	I	Data un-quantified, but fruit set high and seeds viable.	1.5 ± 0.5
	South-central Peloponese (Gerolimenas and Gythio)	I	ditto	1.6 ± 0.3
	Crete, Agia Galini	I	ditto	1.4 ± 0.9
	Crete, Tympaki	I	ditto	1.9 ± 0.5
Ollerton (unpublished data)	Crete, Agios Nikolaos	I	42 ± 23	1.1 ± 0.2
South Africa (Geerts and Pauw unpublished data)	Buffelsrivier	I	61 ± 10	1.4 ± 0.3
	Leipoldtville	I	74 ± 9	-

In its non-native range *N. glauca* is a conspicuous, profusely blooming invasive species growing predominantly along roadsides and on disturbed land in semi-arid regions.

It can be extremely abundant; for example, in Tenerife we have recorded stem densities of 0.7 ± 0.3 m^{-2}, covering hundreds of square metres, and in an extensive population in South Africa (Buffelsrivier) we recorded stem densities of 2.0 ± 0.4 m^{-2}. Similarly, in Israel it forms relatively dense scrub in both mesic and semi-arid regions. These high densities are achieved mainly from seed production; there is no clonal growth, though broken stems can re-sprout and there may be some rooting from horizontal branches in contact with the soil.

Fruit set in populations can be high (Table 1) and each fruit contains hundreds of tiny, dry seeds with viabilities of about 90% (Table 2). Seedlings are common in non-native populations.

THE FLORAL BIOLOGY OF *N. GLAUCA*

Within its native range, the flowers of *N. glauca* are typically yellow and tubular, ranging from on average 32.0 ± 2.2 mm to 41.9 ± 4.9 mm in length (n = 6 populations – see Nattero et al. 2009). The mouth of the corolla is green when the flower first opens, but changes to yellow over several days, until the flower is a single hue (Fig. 1). In scattered

TABLE 2. Seed production and viability in introduced population of *Nicotiana glauca*. Seed germination was assessed by sowing 20 or 25 (in Israel) seeds on damp filter paper in each of 10 Petri dishes.

Region	Mean seeds per fruit ± SD	Number of fruit scored	Seed viability (%)	Number of seeds
Israel	1122.7 ± 655.8	12	92.7 ± 5.2%	250
California	655 ± 247	16	-	-
South Africa	1435.8 ± 1063.6	7	87.5% ± 10.6%	200
Tenerife	-	-	85.5 ± 6.4%	200

FIGURE 1: Stages of flower development in *Nicotiana glauca*. From left to right: closed late stage bud; newly opened flower; older flower showing colour change of mouth of corolla tube from green to yellow. Photograph by Jeff Ollerton in an invasive population on Tenerife.

populations of northwest Argentina, a flower colour polymorphism is present which includes dark red, reddish yellow and yellow morphs.

All non-native populations studied to date possess only the typical yellow flower colour variant which may reflect the introduction of a limited set of genotypes into the alien range (Fig. 1). Corolla length also tends to be shorter in non-native populations than the maximum observed in native populations (up to 57 mm); for example, flowers on Tenerife are on average 37.6 ± 1.7 mm in length (n = 21 flowers from 5 plants); South Africa (Buffelsrivier) = 33.7 ± 0.5 mm (n = 10 flowers on each of 16 plants); California = 35.5 ± 1.8 mm (n = 10 flowers per plant on 85 plants across 4 sites) though island populations (more recently colonized and containing shorter billed hummingbird visitors) have slightly shorter corollas than the mainland plants (Schueller 2007); northern Israel = 34.8 ± 2.0 mm (n = 10 flowers on each of 10 plants); Peru = 33.3 ± 1.5 mm (n = 10 flowers on each of 4 plants); finally, Greek populations have the shortest recorded corolla lengths with an average of 31.8 ± 2.5 mm (n = 95 flowers on 9 plants).

Nectar is abundantly produced and of moderate sugar concentration in both native and introduced populations (Table 3). Sugar composition has been analysed as 48.6%: 38.9%: 13.2% (sucrose: fructose: glucose, Galetto & Bernardello 1993b). Data from non-native populations were obtained using a variety of protocols, e.g. bagged for various periods versus standing crop from open flowers, at various times of the day, making direct comparisons problematic. But they largely agree with the results from the native populations in that they show that *N. glauca* flowers produce moderate to substantial quantities of moderately concentrated nectar (Table 3). A daily rhythm of nectar volume was detected in some populations but this varied. In Israel the lowest volumes were found in the morning and rose in the afternoon, whilst in Gran Canaria the peak was at midday. Perhaps more expected for a bird pollinated plant is the observation of peak nectar volumes in the early morning in a population in South Africa (Table 3).

Although, as we mentioned, the nectar data have been collected using a range of protocols and are therefore not directly comparable, nonetheless these results emphasise our main point that *N. glauca* produces abundant nectar in all populations, even those that are predominantly selfing (see below).

The population mean minimum stigma-anther (S-A) distance is a measure of the average ability of flowers to autogamously self pollinate (e.g. Armbruster 1988). In *N. glauca* in California, island populations have shorter S-A distances than mainland populations. This is probably a result of the initial colonising plants being predominantly selfing rather than a result of natural selection favouring self pollinating genotypes, as the island populations (contrary to expectation) did not experience lower pollinator visitation rates compared to mainland populations (Schueller 2004). However, S-A distances vary greatly among populations (Table 1) and there is a trend of smaller S-A distances when one compares native populations, with non-native populations where specialised bird pollinators are present and populations with no pollinators (Fig. 3). The difference between mean S-A of plants in their native range (2.4 ± 0.9 mm, n = 7 populations) versus those from introduced populations where there are no pollinators (1.5 ± 0.3 mm, n = 6 populations) is small in absolute terms (only 0.9 mm on

TABLE 3. Nectar production in flowers from native and introduced population of *Nicotiana glauca*. All means are ± SD. Status: N = Native, I = Introduced. Unless otherwise cited, see text for details of authors responsible for data collection. Sample sizes, duration of bagging and times of collection vary considerably; details available from first author on request.

	Status	Mean nectar volume (µl)	Mean nectar concentration (%)	Notes
Argentina	N	20.0 ± 8.1	25.2 ± 3.7	Galetto & Bernardello (1993a)
California	I	25.4 ± 16.8	25.1 ± 6.0	
Mexico	I	2.2 ± 5.8	36.0 ± 1.7	Hernández (1981)
Peru	I	12.7 ± 12.1	20.2 ± 5.8	
South Africa	I	15.5 ± 14.4	26.9 ± 4.0	at 08h30
		2.8 ± 4.7	31.8 ± 6.4	at 14h30
Tenerife	I	5.7 ± 4.7	26.8 ± 7.4	
Gran Canaria	I	4.9 ± 2.8	34.4 ± 8.4	at 09h45
		9.0 ± 8.9	44.0 ± 14.6	at 12h00
		1.5 ± 2.2	27.1 ± 27.6	at 15h45
Greece	I	23.5 ± 8.6	-	
Israel	I	5.7 ± 3.4	20.4 ± 1.0	at 08h00
		9.8 ± 3.8	19.9 ± 3.7	at 14h00

average). But in proportional terms this represents a decrease in stigma-anther distance of over one third from plants in the native ancestral range to the introduced invasive populations.

The small S-A distances of invasive compared to native populations may play a role in the ability of invasive populations to produce greater proportional fruit set (Table 1) as on average introduced populations have statistically significantly (at $P = 0.06$) greater reproductive output than native populations [mean fruit set: Native = 42.4 ± 13.1% (n = 7 populations); Introduced = 57.3 ± 16.9% (n = 12 populations); independent samples t-test: t = -2.0, df = 17, $P = 0.06$]. However, there is some geographical variation to this pattern; for example, self pollination in Israel is rare and occurs in only 6% of bagged *Nicotiana glauca* flowers (Tadmor-Melamed 2004), bagged flowers in a Mexican population studied by Hernández (1981) did not set fruit, whilst within California populations, mean fruit set of bagged flowers varied from 6 to 29% (Schueller 2004).

FLOWER VISITORS TO *N. GLAUCA*

In its native range in South America, *N. glauca* is pollinated by several species of hummingbirds and nectar robbed by *Xylocopa* carpenter bees (Table 4). In addition, the hummingbird *Chlorostilbon aureoventris* behaved as a secondary nectar robber in a population from northern Argentina and as a legitimate pollinator in others (Table 4). None of these hummingbirds, nor the *Xylocopa*, are *Nicotiana* specialists: all visit the flowers of other plants for nectar.

Outside of its native range, two distinct patterns emerge, depending upon whether or not the populations establish within the range of specialist flower visiting birds. In Argentina, Peru, the south western USA and Mexico, hummingbirds once again act as pollinators, with bees and flies also making occasional legitimate visits to flowers (Table 4). In addition, the flowers are nectar robbed by native bees, honeybees (Fig. 2), hoverflies (Syrphidae) and flower piercers of the genus *Diglossa*. In Israel, sunbirds (*Nectarinia osea*) are likely to be the main pollinators: 60% of their visits were legitimate, with nectar being accessed from the front of the flower; in the other 40% of visits the birds pierced the corolla base, and thus acted as nectar robbers. The Hummingbird hawkmoth (*Macroglossum stellatarum*) was also observed as an occasional legitimate visitor in Israel, with *Xylocopa* and also several species of ants acting as nectar robbers (Cohen et al., pers. obs.; see Table 4). In South Africa, three species of sunbirds, the Malachite sunbird (*Nectarinia famosa*), the Dusky sunbird (*Cinnyris fuscus*) and the Southern double-collared sunbird (*C. chalybea*) have been confirmed as pollinators (Geerts & Pauw 2009). The former species is the most effective and frequent pollinator, while the latter two species also rob during 7% and 61% of visits respectively. There are also records of flower visitation of honeyeaters for Australia but their role in pollination is not clear (Table 4).

In the northern Mediterranean and Tenerife, where there are no specialist flower visiting birds, flower visitors have never been observed in any populations, despite extensive observations (Table 4). For example, five contrasting populations in the arid south west of Tenerife were surveyed during peak *N. glauca* flowering in April 2006. These populations had different abundances and densities of plants, and ranged from suburban post-demolition sites to rural, goat-grazed habitats. Despite the presence in all of these habitats of potential flower visiting

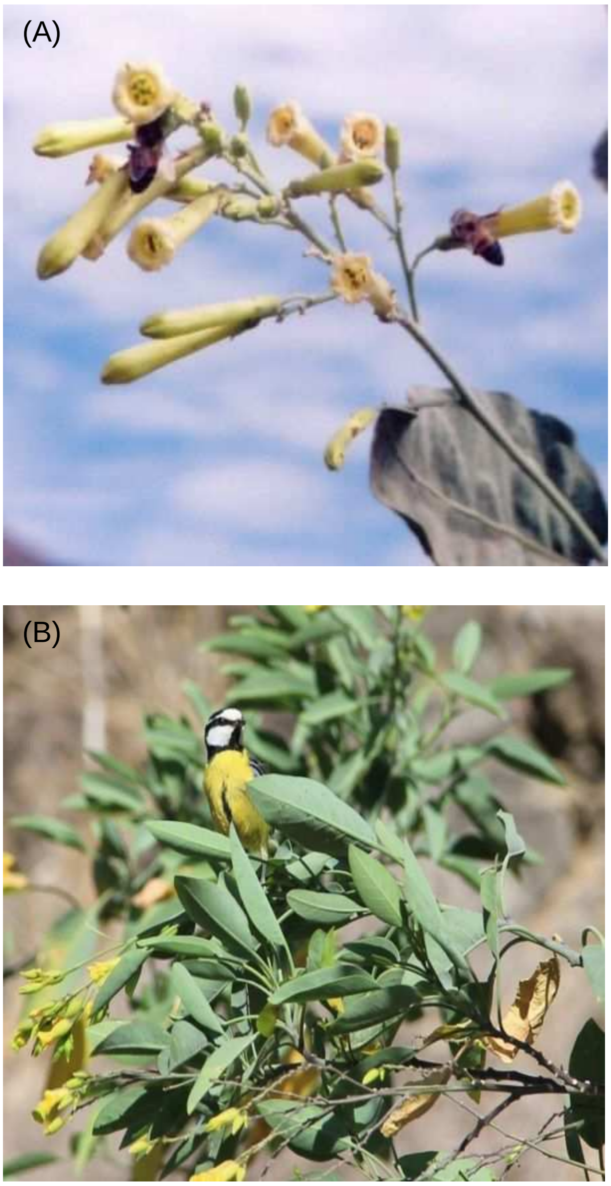

FIGURE 2: (A) Flowers of *Nicotiana glauca* being nectar robbed by introduced honeybees (*Apis mellifera*) in a non-native population in the high Andes of Peru. Photograph by Stella Watts. (B) A Canary Island blue tit (*Parus teneriffae*) observed robbing flowers for nectar on Gran Canaria in 2012. Photograph by Jane Stout

insects (including bees and butterflies) and birds (principally the Canary chiffchaff *Phylloscopus canariensis* a generalist bird that opportunistically visits other flowers for nectar – see below) visits to flowers were never observed. In addition we checked over 1600 flowers (on average 330 per population) and found no evidence of nectar robbing.

Finally, one population was surveyed for nocturnal visitors, particularly large night-flying moths, on three evenings. This population was chosen because of the presence of larvae of the Barbary spurge hawkmoth (*Hyles tithymali tithymali*) feeding on *Euphorbia broussonetii*, indicating that these potential pollinators were present in that community. As well as checking flowers with flashlights, we added fluorescent dye powder (see Kearns & Inouye 1993; Dafni et al. 2005) to 10 flowers on each of 4 trees on one evening. On the two subsequent evenings we checked for dye transfer to nearby flowers but none was observed. These results confirmed previous observations by Ollerton et al. in 2003, 2004 and 2005 that *N. glauca* flowers on Tenerife are rarely, if ever, visited by nectar-feeding animals. These results strongly suggest that Tenerife populations are wholly selfing.

In contrast, observations in 2012 in Gran Canaria revealed a range of insects and passerine birds visiting the flowers of *N. glauca* at one site (Table 4, Fig. 2). This is surprising given the observations made on the nearby island of Tenerife. However, it is worth noting that the winter of 2011-12 was one of the driest experienced by the Canary Islands since records began. Some plant species failed to flower and others flowered much later than usual, resulting in flowers being visited by insects that are not normally seen on them (Ollerton, unpublished data). It is possible that the Gran Canaria observations were of visitors utilising less favoured flowers as a nectar/water source.

DISCUSSION

In its native range, *Nicotiana glauca* usually forms dense stands only in disturbed sites with recent soil exposure, for example dry river beds and road sides (Nattero & Cocucci 2007). Outside of its native range *N. glauca* is clearly a successful invasive weed of disturbed areas where it forms dense, monodominant colonies because of the high rate of fruit and seed set, the viability of seeds and the frequent recruitment of seedlings into the population.

The pollination system of *Nicotiana glauca* in its native range can be best described using the terminology of Fenster et al. (2004) and Ollerton et al. (2007) as functionally specialized for hummingbird pollination, but ecologically generalized in that a range of hummingbird species can act as pollinators (Nattero et al. 2010). In this respect it seems to be an unlikely candidate as an ecologically invasive species, in relation to its ability to co-opt other non-hummingbird pollinators (Richardson et al. 2000; Olesen et al. 2002). In parts of Argentina, Peru, Mexico, California, South Africa and Israel, where *N. glauca* has been introduced for at least 100 years, the species is clearly well integrated into the local pollination web via its interactions with specialist flower feeding birds including hummingbirds (Hernández 1981; Schueller 2004, 2007) and sunbirds (Tadmor-Melamed et al. 2004; Geerts & Pauw 2009).

The successful pollination of *N. glauca* by sunbirds in the Old World comes as a surprise. Like many other hummingbird pollinated New World flowers, the flowers of *N. glauca* are oriented towards open space, an adaptation for pollination by birds that hover while feeding. According to conventional wisdom, Old World birds perch while feeding, so Old World flowers need to be oriented towards a perch in order to receive

TABLE 4: Flower visitors to *Nicotiana glauca* within its native range and in areas where it is introduced. "Legitimate flower visitors" are those which enter from the front of the flower and are the most likely pollinators; flower robbing visitors pierce holes at the base of the corolla to access the nectar, or make secondary use of previously excavated holes.

Range and locality	Legitimate flower visitors	Flower robbing visitors
Native – within the range of specialist flower visiting birds		
Argentina and Bolivia (6 sites - Nattero & Cocucci 2007, Nattero et al. 2010)	Hummingbirds (4 spp.)	*Xylocopa ordinaria* *Chlorostilbon aureoventris*
Introduced – within the range of specialist flower visiting birds		
Peru (3 sites within the Sacred Valley during February, June and August 2002 - SW, unpublished data)	Hummingbirds (5 spp.)	*Bombus* sp., *Xylocopa* sp. and other native bees, *Apis mellifera*, Syrphidae, *Diglossopis cyanea*
USA California (4 sites - Schueller 2004) California, Sonara and Sinaloa (Stiles 1973, 1976)	Hummingbirds (3 spp.) Bees and Diptera (very infrequently) Hummingbirds	House finches and white-crowned sparrows observed pecking at flowers and usually destroying them or ripping corolla; also occasional holes at base of corolla made by unknown bee and frequently find ants in flowers that consume a lot of the nectar, but do not act as pollinators.
Israel (Tadmor-Melamed 2004, Tadmor-Melamed et al. 2004, Cohen 2007)	Palestine Sunbirds (60% of 274 visits were legitimate Hummingbird hawkmoth (*Macroglossum stellatarum*)	Palestine Sunbirds (40% of 274 visits were nectar robbery) *Xylocopa pubescens* *Apis mellifera* (secondary nectar robber) Seven ant species (Formicidae)
South Africa (Skead 1967, Knuth 1898-1905; Marloth 1901; Geerts & Pauw 2009; SG, unpublished data)	Malachite sunbirds (*Nectarinia famosa*) Dusky sunbirds (*Cinnyris fuscus*) Southern double-collared sunbirds (*Cinnyris chalybea*)	*C. chalybea* and *C. fuscus* Weavers (*Ploceus capensis* and *P. velatus*) destroy flowers to access nectar
Australia (Hobbs 1961)		White-fronted honeyeater (*Phylidonyris albifrons*)*
México (1 site Hernández 1981)	Hummingbirds (4 spp.)	*Diglossa baritula* and *Xylocopa* sp.
Argentina (3 sites - Nattero & Cocucci 2007)	Hummingbirds (3 spp.)	*Xylocopa ordinaria*
Introduced – outside of the range of specialist flower visiting birds		
Tenerife (5 sites in the arid south west - Ollerton et al. unpublished data)	None observed	None observed > 1000 flowers checked
Gran Canaria (one site in the Arguineguin Valley – Stout unpublished data)	Solitary bees (2 spp?) Neuroptera	Common whitethroat (*Sylvia communis*) Canary Islands blue tit (*Parus teneriffae*) Both bird species were observed removing flowers from plants, then pecking a hole in the base of the corolla to drink nectar before dropping flowers to the ground.
Crete, Agios Nikolaos (Ollerton unpublished data)	None observed	None observed on c. 200 flowers
Greece (Schueller unpublished data)	None observed	None observed

*Hobbs (1961) does not indicate if visits were legitimate. The short, broad bill of this species suggests that it acts as a robber (B. Lamont pers. com.).

pollination (Westerkamp 1990). Unexpectedly, Old World sunbirds were found to adapt their behaviour and hover for extended periods of time while feeding from the hummingbird adapted flowers of *N. glauca* (Geerts & Pauw 2009) though it is possible that feeding whilst hovering is under documented (see Janecek et al. 2011). It remains to be determined whether Australian honeyeaters are also able to adopt this novel behaviour and act as pollinators of *N. glauca*.

In the northern Mediterranean and the Canary Islands, in contrast, *N. glauca* has not become integrated into the local flower visitation web, either via pollinators or nectar robbers. There are a restricted number of native Canarian and European taxa which could potentially pollinate *N. glauca*, for example long tongued bees such as *Xylocopa* and *Bombus* (which could also act as nectar robbers), and the larger Lepidoptera, including various hawkmoths (Sphingidae). Non-flower specialist passerine birds, particularly chiffchaffs (*Phylloscopus canariensis* and *P. collybita*), are known to pollinate a number of native Canarian plants (Vogel et al. 1984; Valido et al. 2004, Ollerton et al. 2008), at least one continental European species (Ortega-Olivencia et al. 2005) and are opportunistic feeders at the flowers of other non-native plants (Clement 1995; Ollerton pers. obs.). Their beak and tongue lengths are too short for them to legitimately access the nectar of *N. glauca*; however they are known to nectar rob other plants in the Canary Islands, for example *Aloe* spp. (Bramwell 1982). Extensive observation of populations of *N. glauca* on Tenerife and in Greece revealed no instances of nectar robbery, however. This is despite the presence of chiffchaffs in all populations on Tenerife, some of which were observed to perch in the larger *N. glauca* trees.

The nectar available in flowers of *N. glauca* is a significant energy and water resource for animals in semi-arid habitats. Multiplying the nectar values obtained in Tenerife (see above) by the mean number of open flowers per inflorescence and the mean number of inflorescences per stem, suggests that on Tenerife, each stem on average maintains a standing crop of 374.8 ± 820.7μl of relatively sugar-rich nectar. Using the data for flowering stem densities (above), the nectar resources available to animals that can exploit these flowers would be of the order of 277.6μl m^{-2} in low density areas to 832.9μl m^{-2} in high density areas. We do not know the rate of replenishment of nectar in these flowers in Tenerife (though for an Argentinean population it was 0.2 ± 0.2 ml/h - Galetto & Bernardello 1993a); nonetheless this standing crop represents a large potential resource of energy and water to any flower visiting animals within the semi-arid zone of Tenerife. It far exceeds the standing crops of most native species, with the exception of some of the specialised passerine-pollinated endemics (Ollerton et al. 2008) which are mainly restricted to the wetter laurel forest communities of the island. Why this resource is not utilised, resulting in the subsequent integration of the species into the local flower visitation web, is unclear. It is possible that the alkaloid content of the nectar of *N. glauca* deters animals that might otherwise exploit the nectar (Tadmor-Melamed et al. 2004) which would suggest that pollinators and nectar robbers within the native range of the plant, as well as in California, Israel and South Africa, have digestive strategies adapted to cope with these compounds. The relatively high fraction of sucrose, which can only be digested by specialized nectarivores, i.e. hummingbirds and sunbirds, might additionally deter generalist passerines such as chiffchaffs. These areas deserve further research.

Despite the absence of pollinators in some parts of its modern range, *N. glauca* is a plant which is reproductively successful to the point of being a problematical invasive. High fruit and seed set, and relatively small S-A distances, suggest that these populations are largely selfing; apomixis is unlikely as emasculated and bagged flowers of plants in California never resulted in fruit or seed set (Schueller 2002). The difference in average S-A distances in native versus non-native habitats implies that populations in the native range are less frequently selfing. In native populations in Bolivia, where S-A distance is greatest, and presumably with a long history of interaction with the giant hummingbird (*Patagona gigas*), fruit set is relatively low (Nattero et al. 2010; Loayza et al. 1999). The populations with a small S-A distance therefore have pre-adapted the species to be a successful invader and fits with the ecology of the plant as a weedy colonising small tree of disturbed soil in South America. Nevertheless, despite small S-A distances and high levels of selfing, plants in South Africa that receive visits from sunbirds set significantly more fruit and seeds than pollinator-excluded controls (Geerts and Pauw 2009). The trend of decreasing S-A distances from native populations, to invasive populations that are within the range of specialised flower visiting birds, to those where no birds are present (Fig. 3) is precisely what we would expect if initial founder events by largely self pollinating, isolated individuals are important prior to the establishment of larger populations that then subsequently attract significant numbers of native bird pollinators (if available) or remain as selfing populations if no suitable pollinators exist in the locality.

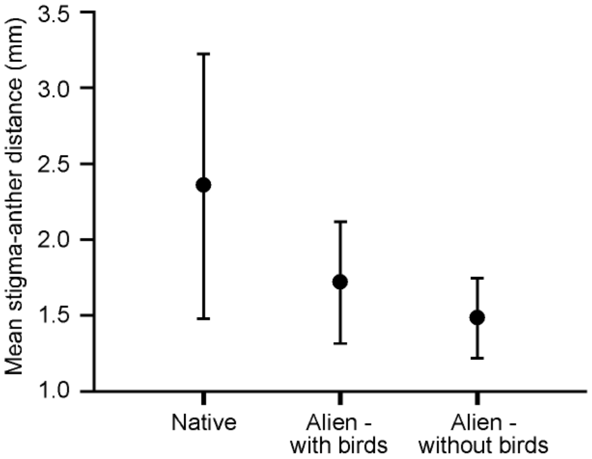

FIGURE 3: Mean (± 95% confidence interval) stigma-anther distance for native populations of *Nicotiana glauca* ("Native" – n = 7 populations) compared to non-native populations within ("Alien-with birds" – n = 11 populations) and outside ("Alien-without birds" – n = 6 populations) of the range of specialised flower visiting birds (hummingbirds and sunbirds). One-way ANOVA: $F_{2,20}$ = 4.4, P = 0.027. Only the contrasts between Native vs. Alien-with birds (LSD post-hoc test: P = 0.03) and Native vs. Alien-without birds (LSD post-hoc test: P = 0.01) are significantly different, but there is an apparent trend and the latter has only a small sample size.

Invasive plants with a high rate of nectar production almost invariably have a high rate of pollinator visits to flowers, for example *Buddleja davidii* and *Impatiens* *glandulifera* in Europe and *Lantana camara* and *Melaleuca quinquenervia* in subtropical North America (Chittka & Schürkens 2001; Koptur 2006). The assumption is that many of these species are likely to be ecological and/or functional generalists in their native habitats (reviewed by Corbet 2006 and Traveset & Richardson 2006; see also Harmon-Threatt 2009; Rodger et al. 2010). For instance, in Europe *Impatiens glandulifera* is a functional specialist but an ecological generalist (it is pollinated by a range of bumblebees *Bombus* spp. – Chittka & Schürkens 2001; Lopezaraiza-Mikel et al. 2007; Nienhuis et al. 2009; Nienhuis & Stout 2009). In its native Himalayan habitats it is also *Bombus* pollinated (Saini & Ghattor 2007) which suggests that this plant was pre-adapted to be a successful invader in terms of its ability to integrate into existing pollination webs containing *Bombus* spp. or functionally equivalent medium to large sized bees.

Invasive species may therefore re-establish their pollination niche only if they can appropriately interact with suitable local pollinators. Intuitively we might consider this to be less likely if the species is an ecological, functional or phenotypic specialist, but the data here are contradictory: functionally and phenotypically specialised ("euphilous") introduced plants were shown by Corbet (2006) to be the most successful group of plants (as measured by range increase) within the British and Irish flora. This may be due to the tendency of gardeners to introduce plants with large, showy flowers. *Nicotiana glauca* was introduced to Tenerife as a garden ornamental in the early 19th Century (Kunkel 1976) and so there would have been ample time for the species to establish relationships with pollinators or nectar robbers if suitable species were available. However in that time *N. glauca* has largely forsaken outcrossing for a successful selfing reproductive strategy. Island ecosystems are especially vulnerable to plant invasions (Simberloff 1995; Olesen et al. 2002) and *N. glauca* is only one of a large number of introduced plant species which may be negatively impacting on the flora and fauna of the Canary Islands and two of the California Channel Islands studied by Schueller (2002). *N. glauca* has some degree of frost tolerance and, whilst adult plants may be killed by very low temperatures, seeds survive to germinate the next year (Ollerton, pers. obs.). Therefore the increasingly arid environments predicted for some regions by future climate change may result in the species spreading even further north in Europe and North America.

In order to test our hypothesis that shorter S-A distances have evolved in invasive populations of *N. glauca* that lack pollinators, further research is required. In particular we would like to know why it is that seeds produced from self pollination show such high viability with no apparent cost from inbreeding depression. In addition, we would like to understand the role of other mechanisms that could prevent or facilitate selfing (such as reduced incompatibility of self-pollen, and synchronization of pollen viability and stigma receptivity) in native and invasive populations with and without pollinators. Finally we require data on the extent to which native populations of *Nicotiana glauca* are pollen limited, the degree of self compatibility amongst individuals and the natural rate of self pollination.

In conclusion, we can state that *Nicotiana glauca* is a successful invasive species outside of its native range, despite its functionally specialised pollination system. In areas where suitable bird pollinators are available, for example hummingbirds in California and sunbirds in South Africa and Israel, *N. glauca* becomes integrated into the local pollination web and sets seed by both out-crossing and selfing. In regions where there are no specialised flower visiting birds, such as the Canary Islands and Greece, abundant seed set is maintained by selfing, and the considerable nectar resources are hardly utilised by native flower visitors, either legitimately or by nectar robbing. In the case of *N. glauca*, invasion success is therefore not predictable from its interactions with pollinators in its native range.

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