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Lantana camara L. (*sensu lato*): an enigmatic complex

Neha Goyal[1], Gyan Prakash Sharma[1]

1 *Department of Environmental Studies, University of Delhi, Delhi–110007, India*

Corresponding author: *Gyan Prakash Sharma* (gyanprakashsharma@gmail.com)

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Abstract

Lantana camara L., considered among the world's worst invaders is in identity crisis and contentiously referred as *Lantana camara* L. (*sensu lato*). Taxonomic ambiguity in *L. camara* L. (*sensu lato*), a species complex is one of the grim caveats behind incompetence of its management efforts. Recognizing the extent of variability within the complex, we aim to highlight the need to circumscribe its composition to bring effective management and control efforts into practice. There is a need for clear terminology to examine weedy, naturalized and/or invasive complex constituents that have been placed under the contentious umbrella of '*L. camara* L. (*sensu lato*)'. The time is ripe for invasion ecologists, cytogeneticists and conservationists to collaboratively focus on disentangling the complex and integrate their knowledge and expertise into management and control programs.

Keywords

Control, genetics, invasive, species complex, taxonomy

Introduction

Lantana camara L. is one of the world's worst ten invaders (Lowe et al. 2000). The copious invader has disseminated rapidly at temporal as well as spatial scale. This widespread invader inhabits a wide range of habitats adversely impacting native plant species diversity and ecosystem functioning (Gentle and Duggin 1997, Sharma et al. 2005, Love et al. 2009a, Sharma and Raghubanshi 2009). Despite profound environmental and economic threats posed by *L. camara* infestations in non-native range, considerable success has not been achieved to effectively control its spread (Cilliers 1983, Bhagwat et al. 2012). Nevertheless, species invasiveness is too complex to be simply predicted and managed (Williamson 1996). However, we anticipate that the prime reason behind the failure to control invasive *Lantana* could be its existence as an unresolved species complex, *L. camara* L. (*sensu lato*). Inability to correctly identify the plant of interest in the complex has incapacitated control measures (Thomas and Ellison 1999, Day et al. 2003a, Urban et al. 2011).

Historically, taxonomy of the genus *Lantana* has been very complicated (Sanders 2006, Love et al. 2009b). Further, recognition of all weedy and/or invasive genets created due to endless episodes of horticultural improvement within the genus is extremely challenging. Over the last two to three decades, a few articles highlighted the seminal concept of addressing different weedy and/or invasive genets [cultivars, variants, sub-species, hybrids, varieties, forms or even allies (*if they exist*); hereafter, referred as complex constituents] as *L. camara* L. (*sensu lato*) (Stirton 1977, Stirton 1979, Sanders 2006, Sanders 2012; for details, see Urban et al. 2011). However, the importance of this concept has been realized in invasion ecology after decades of consistently delimiting all of the invasive complex constituents with the epithet *L. camara*.

Importantly, little information is available on taxonomic identity and genetic makeup of existent complex constituents and their populations. This further makes it difficult to surmise what facilitates their success as invaders. Considerably, complex constituents' invasive success might be ascribed to phenotypic and/or genotypic novelty created by rigorous hybridization events within the complex, their variable response to selection or their differential adaptive plasticity. However, in order to ascertain the key attribute(s) responsible for their invasive success, identification and differentiation of all possible invasive genets in the complex is fundamental. Detailed study of the complex constituents will offer opportunities to answer key questions about plant invasions. Moreover, it may be useful in making informed choices about monitoring their spread throughout the invaded range. The present synthesis will generate an impetus for comprehensive research efforts to study the remarkably diverse species complex in order to appraise control efforts.

Historical events leading to the species complex

Although specific origin of *L. camara* is unknown, some authors have suggested the species to be a native of South America or Mexico (Howard 1969, Spies and du Plessis 1987), while others suggested West Indies as the place of origin (Moldenke 1973, Palmer and Pullen 1995). Studies report that *Lantana* (including *L. camara*) was imported from America to Europe in mid-16th and 17th centuries for its horticultural value (Stirton 1977, Swarbrick et al. 1995). In Europe, the species underwent substantial horticultural breeding, creating hundreds of cultivars of mixed parentage from the introduced stock (Howard 1969). Subsequently, these cultivars traversed to America, Australia, India and Africa in the mid-19th century (Howard 1969, Stirton 1977, Swarbrick 1985, Morton

1994). With time, many cultivars escaped cultivation, spread beyond the ornamental confines of the garden and became weeds (Spies 1984, Swarbrick 1985, Palmer and Pullen 1995). Studies have identified hybridization to contribute substantially to invasiveness, weediness and/or range expansion (Brown and Marshall 1981, Ellstrand and Schierenbeck 2000, Hovick and Whitney 2014). Likewise, innumerable intentional as well as unintentional hybridization events in *Lantana* led to remarkable increase in its complexity. Anthropogenically-induced genetic diversity in the species complex indeed facilitated the species to invade heterogeneous habitats (Cilliers 1983, Bhagwat et al. 2012, Goncalves et al. 2014). The highly invasive species now exists in 60 countries and island groups of Asia, Africa and Australia (Cronk and Fuller 1995, Day et al. 2003b).

Enigma of the species complex

Extensive hybridization followed by polyploidy or polyploidization followed by hybridization events within and between wild, naturalized and cultivated taxa further enhanced complexity leading to the evolution of *L. camara* L. (*sensu lato*) (Sanders 1987, Sanders 2006). Wild complex constituents have also been reported to hybridize and genetically assimilate with the rare native counterparts, threatening the existence of rare genets (see Maschinski et al. 2010). These evolutionary processes have led to enormous phenotypic as well as genotypic variability, which complicates species delimitation in the complex. The ones growing in wild potentially differ morphologically, karyologically, physiologically and ecologically from those prized for their horticultural value, multicolored flowers, and ease of propagation (Spies 1984, Sanders 2006). Therefore, weedy, naturalized and/or invasive complex constituents, broadly referred as *L. camara* L. (*sensu lato*) merit a deliberate taxonomic delineation (Sanders 2006).

Complex constituents can be distinguished morphologically (flower size, shape and color; leaf size, hairiness and color; stem thorniness; height and branch architecture), physiologically (growth rates, toxicity to livestock) and, by their chromosome number, nuclear DNA content (Stirton 1979, Gujral and Vasudevan 1983, Scott et al. 1997) and ploidy level (Stirton 1977, Palmer and Pullen 1995). Studies have also reported leaf anatomical characteristics (Passos et al. 2009) and detailed chemical profiling of foliar chemical constituents (Love et al. 2009b, Sena et al. 2012) as useful markers for supporting species delimitation. However, obscure limits of natural variation hamper workers in the field to effectively classify and disentangle complex constituents. The disputed limits of *L. camara* also complicate identification of the genotypes that have naturalized and are proliferating in the non-native range.

Understanding the species complex

Unlocking diversity in the complex is considered a formidable taxonomic problem (Khoshoo and Mahal 1961, Howard 1969, Moldenke 1971, Spies 1984, Sanders

2006). The complex with a broad spectrum of variability has no record of parental species after 1492 (Stirton 1977). It is highly difficult to deduce putative parents of each constituent in wild as they interbreed freely leading to immense variation in the gene pool (Binggeli 2003, Spies 1984, Urban et al. 2011). Further, ongoing hybridization events in the cryptic complex have blurred taxonomic distinctions of complex constituents and reduced classification accuracy (Sanders 2006, Maschinski et al. 2010). Although the taxonomically uncertain complex has not been subjected to considerable progress till date; a few studies have attempted to reasonably explore the composition and nomenclature to classify the genus *Lantana* through well-devised keys (Munir 1996, Rajendran and Daniel 2002, Méndez Santos 2002, Sanders 2006, Sanders 2012).

Cytological studies on different populations of *Lantana* have reported basic chromosome numbers to be 11 & 12 (Henderson 1969, Sinha and Sharma 1984) and 8 & 11 (Moldenke 1983). They have also pointed out the existence of polyploid series in the genus based on reported base numbers. Highest chromosome number was reported as 2n = 72 (Natarajan and Ahuja 1957), and 2n = 66 (Bir and Chatha 1983), while 2n = 22 was recorded to be the lowest (Sen and Sahni 1955, Sanders 1987). Basic chromosome numbers of 11 & 12 have been recorded, with ploidy levels ranging from diploid to hexaploid in *L. camara* (Tjio 1948, Spies 1984, Ojha and Dayal 1992, Munir 1996, Brandao et al. 2007). Frequent hybridizations between different ploidy levels have also been reported (Spies 1984). Existence of multiple polyploidization pathways has been considered to contribute towards enormous complexity in *L. camara* (Czarnecki II and Deng 2009).

Rapid adaptive evolution and genetic change have been proposed to contribute significantly to the success of invasive species in the introduced range (Prentis et al. 2008, Prentis and Pavasovic 2013). Studies have revealed significant information regarding genetic variation, population differentiation, and introduction history of a few invasive species using molecular markers (Chun et al. 2010, Thompson et al. 2012, Vardien et al. 2013). Few studies have also attempted to explore range expansion of *L. camara* in different countries (Vardien et al. 2012, Ray and Quader 2014). Microsatellite markers developed for *L. camara* have also been successfully used in assessment of genetic variation and population structure in India, broadening understanding on dynamics of its introduction, range expansion and gene flow (Ray and Quader 2014, Ray and Ray 2014). Ray and Quader (2014) identified that the present diversity of *L. camara* in India is an output of multiple introduction episodes followed by gradual spatial expansion with the recurrent gene flow. Recently, Ray and Ray (2014) studied genetic variation in *L. camara* in India and synthesized that the species consists of two genetic clusters, representing emerging ecotypes across space that could be differentially adapted to local habitat conditions. Broadly, these studies have revealed high genetic diversity in *L. camara* and have tried to elucidate past dispersal patterns (Vardien et al. 2013, Ray and Quader 2014, Ray and Ray 2014). Further, these markers can be useful in addressing several questions about breeding system, pollination and dispersal of the species (Ray et al. 2012). However, to improve our understanding of the range expansion of the complex, there is a need for further research at a global scale that examines genetic and genomic attributes of the complex constituents. It is highly essential to understand the genetic system of a taxon as it affects the nature and extent of variability, evolutionary processes and pathways which may further affect invasiveness.

Unresolved species complex: an impediment to management efforts

Interestingly, a large proportion of invasive alien plants are those that were introduced as ornamentals (Mack and Lonsdale 2001, Foxcroft et al. 2008). In general, ornamental plants selected for introduction pose a high invasion risk as they possess traits such as high fruit/seed production, high growth rate, and tolerance to a wide range of environmental conditions (Anderson et al. 2006).

Highly variable *L. camara* is one amongst those introduced ornamental species that has a wide scale of distribution. In spite of longer residence time, there is a dearth of scientific studies integrating its history, spread, ecological impact, evolution, and management. Thus, attempts to control the invader using mechanical, chemical and biological means have met with limited success (Morton 1994, Thomas and Ellison 2000, Day et al. 2003a). Additionally, this can also be attributed to a gamut of complex constituents that differ in their distribution, habitat preferences, weediness, morphology, chemical constituents, toxicity to livestock, susceptibility to herbicide treatment, and susceptibility to bio-control agents (Smith and Smith 1982, Cilliers and Neser 1991). Further, success of bio-control agents employed in controlling *L. camara* (including all weedy and/or invasive complex constituents) may vary from one location to another owing to differential feeding habits of the bio-control agents, their host-specificity, climatic suitability, and plant-insect interactions (Broughton 2000, Zalucki et al. 2007). Biological control measures are principally constrained by our confounding understanding of the broad spectrum of phenotypic and genotypic variability present within the complex. However, genetic analysis of the complex can aid in identification of potential control agents to be specifically targeted (Scott et al. 2002).

Future directions

Under the current scenario of genetic diversity and associated taxonomic ambiguity, distinction of genets in *L. camara* L. (*sensu lato*) is highly dubious. However, a few studies erroneously address invasive *Lantana* with ambiguous identity as *Lantana camara* L. or *Lantana camara* L. (*sensu stricto*), which is extremely misleading with the current understanding of the complex. Merely considering *L. camara*, representative of all troublesome weedy genets in the whole complex, will neither ensure understanding all of the myriad invasive traits, nor would it serve to appropriately answer management questions. Hence, studies pertaining to invasive *Lantana* should address the individuals in the wild with the epithet '*L. camara* L. (*sensu lato*)' (Stirton 1977, Neser and Cilliers 1990, Munir 1996, Baars and Neser 1999, Day and Zalucki 2009). Referral of the invasive complex constituents broadly as *L. camara* L. (*sensu lato*) is considered correct under both the International Code of Botanical Nomenclature and the International Code of Nomenclature for Cultivated Plants (see Urban et al. 2011).

To circumscribe the complex constituents, documentation of appropriate suite of distinguishing characters of complex constituents might facilitate delineation of the considerable variation existing in the complex. A consistent terminology based on morphology, cytology, and genetic attributes using advanced molecular techniques such as DNA-based molecular marker techniques, *viz.* random amplified polymorphism DNA (RAPD), inter simple sequence repeat (ISSR), amplified fragment length polymorphism (AFLP), quantitative trait locus (QTL) mapping, etc. can be devised to explore the genetic diversity of the complex constituents. Integrating the knowledge of plant morphology and chromosome number can also aid in species delimitation, as complex constituents have been reported to behold varying chromosome complements. Attempts to investigate total spectrum of variation using DNA C-values by flow cytometry can be extremely helpful to unravel the diversity in the complex (Suda et al. 2014). Though highly desirable, yet the extremely difficult task of ascertaining absolute taxonomic status to each of the complex constituents can be resolved by estimation of their genome sizes. Variation in chromosome numbers in genus *Lantana* encourages the use of genome size as a species-specific marker. Genome size has been well-applied to resolve notable species complexes such as *Reynoutria* (Mandák et al. 2003); *Knautia arvensis* (Kolář et al. 2009); *Dryopteris carthusiana* (Ekrt et al. 2010); *Callitriche* (Prančl et al. 2014) and, identification of invasive alien taxa (see Suda et al. 2010). Further, documentation of population cytotype structure of the invasive genets and their geographical distribution is central to monitor complex constituents' invasion potential.

High diversity in the complex and continuing hybridization events may potentially broaden its ecological tolerance in climatically suitable as well as unsuitable areas (Goncalves et al. 2014). Furthermore, realizing remarkable spread and better performance of the invasive genets in warmer areas, it is highly probable that invasive *Lantana* will increase its expanse noticeably in future climate change scenarios (Zhang et al. 2014). Control of the invader would be quite challenging in future scenarios of global change. Lack of knowledge about actual genetic diversity in the complex will further undermine all efforts to regulate species' invasion dynamics.

Concluding remarks

The study warrants that there is an urgent need to resolve the species complex to ensure concerted management and timely control over its proliferation. In a nutshell, future of efforts to control invasive *Lantana* lies with resolution of the species complex. There is an urgent need to disentangle the complex to decipher the niche adaptation and range expansive modifications that distinct complex constituents underwent over the evolutionary timeframe. Using insights, we can build-up and enhance our understanding of different facets of *L. camara* L. (*sensu lato*) invasion in entirety.

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