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Authors: Burke, Janelle M., and DiTommaso, Antonio

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Invasion Alert

Corallita (*Antigonon leptopus*): Intentional Introduction of a Plant with Documented Invasive Capability

Janelle M. Burke and Antonio DiTommaso*

Corallita (*Antigonon leptopus*) is a perennial vine, lauded as an ornamental for its vigorous growth, and plentiful (usually) pink flowers, and even its ability to smother unsightly landscapes. In the United States it thrives in horticultural zones 8 to 10, and also is successfully grown worldwide in tropical climates. When corallita is neglected, it can grow quickly over other vegetation, spreading beyond its area of introduction. Once established, it is difficult to eradicate because it produces many tuberous roots that can propagate vegetatively. Its fruits are buoyant, allowing for successful seed dispersal in water. The islands of Guam (South Pacific Ocean) and St. Eustatius (Caribbean Sea) represent two regions where corallita has become so pervasive that it threatens local diversity. In Florida, already it is classified as a Category II invasive. Our report reviews the literature and past studies of corallita, in addition to adding new taxonomic and distribution information from herbarium specimens to clarify the identity and geographic range. It is recommended that introductions of this plant by the horticultural industry in both tropical and temperate regions be closely monitored to prevent spread. On tropical island nations, we advise against any new introductions.

Nomenclature: Corallita; coral creeper; Mexican creeper; corallina, bellisima; *Antigonon leptopus* Hook. & Arn.
Key words: Ornamental, Polygonaceae, tropics, vine.

Like many other members of the Polygonaceae [e.g., *Reynoutria japonica* Houtt., *Emex spinosa* (L.) Campd., *Persicaria perfoliata* (L.) H. Gross], *Antigonon leptopus* Hook. & Arn. (corallita) is documented as an invasive species of natural areas (Ernst and Ketner 2007; Pichardo and Vibrans 2009; Raju et al. 2001). It climbs using tendrils, and persists vegetatively by producing numerous tubers (Pichardo and Vibrans 2009). The flowers are visited by a myriad of pollinators (bees, flies, hummingbirds, butterflies), facilitating sexual reproduction outside of its natural range (Raju et al. 2001).

Corallita is native to Mexico and is cultivated as an ornamental for its showy flowers (Figure 1), and has been introduced across the tropics. It is a reported pest from the South Pacific to Africa and India (Raju et al. 2001). It is a roadside weed in its native Mexico (Howard 2001; Pichardo and Vibrans 2009), but it is on tropical islands where corallita has become most pervasive and problematic (Figure 2). On Christmas Island (Indian Ocean), corallita is reported as "…rampant on sea and inland cliffs and in previously mined areas …where it may be hampering the annual migration of crabs and interfering with natural regeneration" (Swarbrick and Hart 2000). On St. Eustatius, the vine is particularly pervasive, smothering whole areas of vegetation and killing the undergrowth (STENAPA 2007). It has been estimated to cover 20% of the island of St. Eustatius (Caribbean Sea) (STENAPA 2007), and on Fiji (Pacific Ocean) and Christmas Island (Indian Ocean), it is a documented threat to the local flora (PIER 2009; Swarbrick and Hart 2000). In the United States, it is hardy in horticultural zones 8 to 10 (Scheper 2004) and is commonly cultivated in Arizona, Florida, Hawaii, Louisiana, New Mexico, South Carolina, and Texas (Freeman and Reveal 2005).

This invasion alert aims to summarize the current knowledge of the natural history and invasive biology of corallita and call attention to its invasive potential.

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* Ph.D. Candidate, Department of Plant Biology, and Associate Professor, Department of Crop and Soil Sciences, Cornell University, Ithaca, NY 14853. Corresponding author's E-mail: jmb328@cornell.edu

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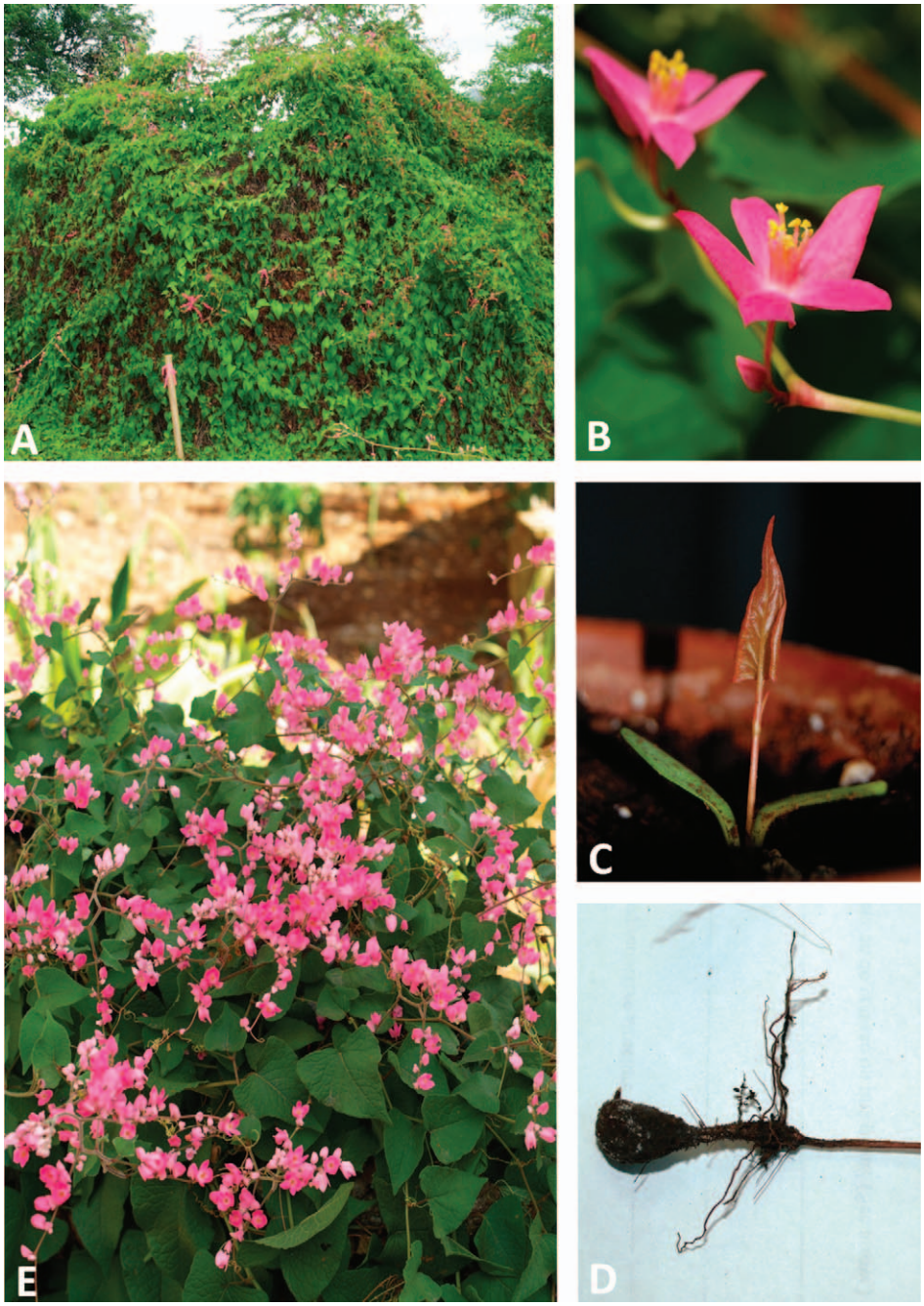

Figure 1. Images clockwise from top left: (A) Habit of *Antigonon leptopus* on roadside in St. Eustatius. (B) Detail of flower. (C) Seedling with cotyledons and first leaf. (D) Tuberous root produced from seedling. (E) Detail of inflorescence and leaf morphology. All photos by J. Burke.

Natural History, Taxonomy, and Distribution

Plant Traits. Corallita is a perennial vine, climbing by tendrils at the end of the inflorescence axes. The base of the plant can become slightly woody with age. Stems are pentagonal in cross section, commonly 1 to 3 m long (3.3 to 9.8 ft) (although they can reach 9 to 12 m in length; Scheper 2004), and quickly sprawl over surrounding vegetation. Leaves are alternate and usually 10 to 16 cm (3.9 to 6.3 in) long. Leaf shape is variable, but usually is deltoid or cordate, the apex acute or acuminate (Figure 1E; Duke 1960). An individual plant can propagate underground via roots, or spread above ground by the production of stolons. Plants easily persist in the soil by producing tuberous roots (Figure 1D), formed from an extensive root crown. Tuberous roots can range in size from

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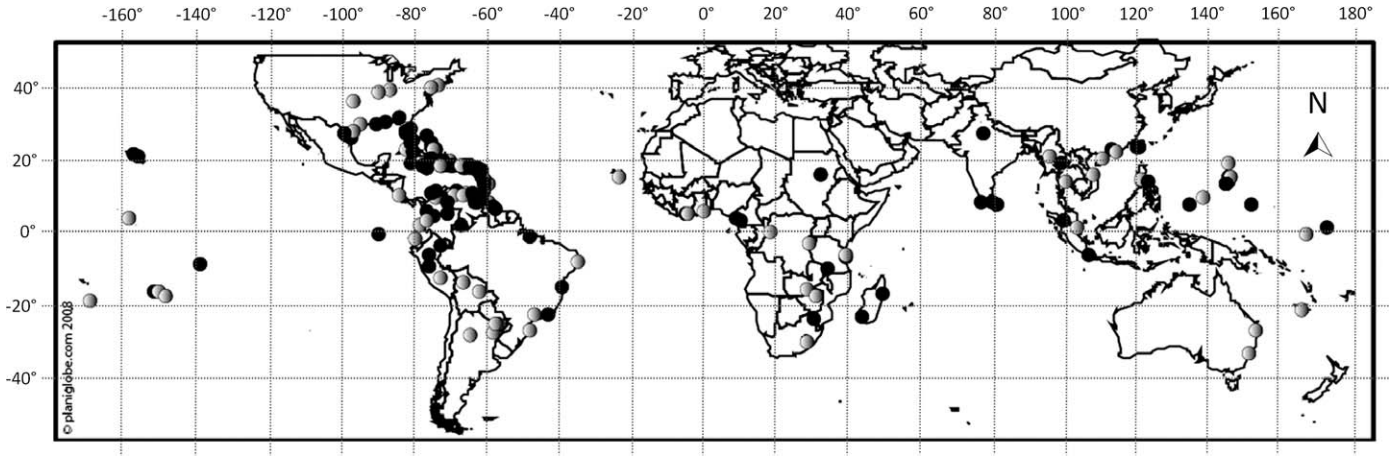

Figure 2. Global geographic distribution map of *Antigonon leptopus*, excluding Mexico and Central America (its native range). Filled circles represent a collection of a plant growing spontaneously; gray gradients circles indicate cultivated specimens. Distribution data were drawn from herbarium specimens from BH, F, MO, NY, P, TEX, and US (standardized herbarium acronyms from Index Herbariorum, 1990).

< 0.5 g to 300 g (0.02 to 10.6 oz) (Ernst and Ketner 2007), but can reach 1.0 to 1.5 kg (2.2 to 3.3 lb) in older plants (Englberger 2009).

The flowers of corallita are arranged in long, branching inflorescences, which are quite striking when hanging over a trellis or fence. The flowers are 0.4 to 2 cm in diameter (Ewing 1982), with five tepals, these light pink to deep pink, magenta, or almost red (Figure 1B). There also is a white-flowered cultivar, although commonly it is not invasive. Eight stamens are fused into a column; at the base of this column copious nectar is produced. The tepals enlarge after fertilization, become papery in texture, and surround the fruit. The fruits are achenes, 0.6 to 1.0 cm long, trigonous, acute and winged at apex, brown, dull, and buoyant. The seed is large, and comprises 70% of the fruit weight (Jones and Earle 1966), and includes ruminate endosperm. Chromosome counts for *A. leptopus* vary from $2n = 14$, 40 to 48 (Freeman and Reveal 2005). The base number for the Polygonaceae likely is $x = 7$ (Brandbyge 1993), suggesting that corallita (and possibly the whole genus) is of polyploid origin.

Taxonomy. All species within the genus *Antigonon* are perennial vines, which can become semiwoody at the base. The native range of this genus extends from western Baja California south to Costa Rica (Duke 1960). Other species of *Antigonon* often are cultivated, both within and outside their native range, for their showy flowers and prolific nectar production (Duke 1960; Ortíz 1994; Pichardo and Vibrans 2009), although corallita is the only species which thus far has been documented as an invasive.

Species delimitations in *Antigonon* have been taxonomically difficult with one to eight species recognized by different taxonomists (Brandbyge 1988, 1993; Graham and Wood 1965), although four species has been the common consensus (Duke 1960; Ewing 1982; Standley and Steyermark 1946). Corallita (*Antigonon leptopus*) is the most morphologically variable and geographically widespread. In contrast, *A. amabile* W. Bull, *A. cordatum* M. Martens & Galeotti and *A. platypus* Hook. & Arn. are relatively well-defined, based on morphological characters and geographic distribution. The native ranges of the four species overlap to some extent; specifically corallita overlaps with *A. platypus* and *A. cordatum* in Mexico. Corallita can be distinguished from the latter species by the leaf petiole: corallita has a slender petiole, whereas the petiole of *A. platypus* and *A. cordatum* is winged, with the leaf lamina decurrent along the petiole. Leaf blade size and shape are phenotypically plastic (shape in particular is correlated with sun exposure) and thus are not reliable taxonomic characters.

Putative hybrid populations between corallita and *A. platypus* have been discovered in Oaxaca and Jalisco, Mexico (Burke, unpublished data). Results from comparative morphological studies suggest that invasive populations of *A. leptopus* are not of hybrid origin because they lack diagnostic characters of *A. platypus*, namely the winged petiole and small flowers. Ongoing taxonomic study by J. Burke (unpublished) has focused on species delimitation as part of a taxonomic revision of *Antigonon*. A complete taxonomic treatment, including species descriptions, distribution, and key to species is forthcoming.

Distribution. The native range of corallita has been unclear because it is cultivated as an ornamental and also is a roadside weed within Mexico (Pichardo and Vibrans 2009), Central America, and the Caribbean. Herbarium collections have helped to clarify the history of introduc-

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tion of corallita through cultivation, and thus to infer its native distribution. Herbarium data suggest that corallita (and other congeners) have been introduced in the Caribbean since at least the mid-19th century. Earliest herbarium records of corallita in the Caribbean come from private gardens, often with a notation about naturalization or escape at a homestead. Based on these data, we have determined corallita is native only to Mexico where it occurs throughout most of the country except at elevations above 1,000 m (3,281 ft). The global geographic distribution of corallita outside its native range is shown in Figure 2. A list of vouchers for spontaneous occurrence worldwide is found in Appendix 1. This list documents the geographic distribution by locality, as well as the oldest-known herbarium specimen at each locality.

In the United States, corallita is cultivated in the southeastern and southwestern regions of the country. It has become naturalized in Alabama, Florida, Georgia, Hawaii, Louisiana, and Texas (Appendix 1), and is cultivated as an ornamental in Arizona, California, Mississippi, New Mexico, North Carolina, and South Carolina. The authors' host herbarium, the L. H. Bailey Hortorium (BH), is unique in its emphasis on cultivated material. From these specimens, we have learned that corallita frequently was cultivated in botanic garden greenhouses since the early part of the 20th century: Fairchild Tropical Botanic Garden, Miami (year 1945, *Dress 1256* [BH]), Missouri Botanic Garden (1914, *Thompson 43* [MO]), and New York Botanical Garden (1904, *Muller s.n.* [NY]). There even is a specimen from 1881, although only with the annotation ''Botanic Garden'' and no specific locality (*Smith s.n.* [US]). Other notable collections at the United States plant introduction garden in Miami (1916, *Popenoe 6* [BH]) and at P. J. Beckman's Company greenhouse in Augusta, Georgia (1917, *Bailey s.n.* [BH]) suggest that this plant was being tested for introduction into the horticultural market early on. The earliest record we have for a naturalized population in the US is in Harris Co., Texas in 1914 (*Fisher 208* [US]).

Phenology. In areas in Mexico where there is a pronounced dry season, *Antigonon* species have a distinct flowering period following the first spring rains (February to April), although flowers can be produced year-round with adequate rainfall. After conducting a year-long study on the phenology of corallita on St. Eustatius, Ernst and Ketner (2007) failed to identify a distinct flowering season, likely due to the lack of a dry season. In tropical climates, this species usually flowers year-round (Raju et al. 2001), whereas in more temperate regions (Arizona, Texas), the foliage senesces during the winter months (Scheper 2004).

Names and Uses. Corallita is a common name for *A. leptopus* in the Caribbean. In Mexico, bellísima is the most frequent common name, although it is used to refer to other species in the genus as well. In the United States, common horticultural names are queen's wreath and Mexican creeper, along with confederate vine. In the South Pacific, chain-of-love commonly is used, although names such as mountain rose and hearts-on-a-chain also are used.

In Mexico, corallita is planted as an ornamental, or as nectar source for honey production. It also is used for decoration in homes or altars in churches (Ewing 1982). The nutty-flavored tuberous roots are reported to be eaten in Mexico and Guatemala (Standley and Steyermark 1946), although recently researchers have tried to consume the roots and found them to be inedible (N. Esteban, STENAPA, personal communication). In Thailand, corallita often is grown as an ornamental, and is found in bridal bouquets and salads. In other introduced regions, its most popular attribute is its vigorous growth, and is used to cover fences or as an ornamental in home gardens.

Invasive Significance

Although its distribution is well documented, there are few empirical studies to date of corallita's ecological impact as an invasive plant. Many reports of the detrimental effects of this plant are anecdotal. The most severe infestations have been found on islands. In Guam (Pacific Ocean), it is common on sea shores, climbing and smothering native vegetation (Space and Falanruw 1999). On Christmas Island, it has been documented to interfere with migrating crabs (Swarbrick 1997). The species is most abundant and problematic on the island of St. Eustatius, where corallita covers at least 20% of the island (Ernst and Ketner 2007). The increased abundance of this plant has prompted the implementation of management efforts in these affected regions. Some governments have initiated legislative action. For example, the Florida Exotic Pest Plant Council has established corallita as a Category II weed (FLEPPC 2009): an invasive exotic which has become more prevalent, but not yet a threat to local plant communities. Australia has placed corallita on a list of documented pests (WWF–Australia 2006). On St. Barthélemy in the Caribbean Sea, inhabitants are fined if corallita is found in their home gardens (Ernst and Ketner 2007).

Habitat. Corallita can grow in almost any soil type, is quite drought tolerant, and also tolerates poor soils (Gilman 2007). The preferred soil pH ranges from 5.0 to 5.5 (Ernst and Ketner 2007). The plants prefer full sun (Ernst and Ketner 2007; Scheper 2004), but also can be found in partial shade. As a tropical plant, corallita does not tolerate temperatures below −7 C (19 F).

Dispersal. Seeds are buoyant, allowing for dispersal after rain storms. Livestock and insects are more likely seed predators than dispersers. For example, in a livestock

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feeding experiment on St. Eustatius, no viable seeds were recovered in the dung of animals when fed corallita fruits (Ernst and Ketner 2007). Locally, tubers are another possible means of introduction into new areas. Smaller tubers and roots easily can be transported to a new location with contaminated soil. This is a similar clonal mode of introduction into new areas as another aggressive weed in the Polygonaceae, *Reynoutria japonica* [= *Fallopia japonica* (Houtt.) Ronse Decr.] (Japanese knotweed).

There is no evidence for long-distance dispersal by any vector besides humans. Ship ballast is a possible unintentional mode of introduction; however the tolerance of corallita seeds to salt water, especially long-term exposure, needs to be evaluated. Even in remote areas of the South Pacific, plants are cultivated as ornamentals (as inferred by herbarium labels). Because we only have evidence as to the intentional introduction of corallita across the tropics, but none for animal, wind, or water dispersal, we suspect that the establishment of new corallita populations in distant localities is the result of intentional introduction through cultivation, with subsequent local naturalization.

Control. Our knowledge of corallita control is limited to two studies: Ernst and Ketner (2007) on St. Eustatius (Caribbean) and Englberger (2009) on Pohnpei (South Pacific). Mechanical control is an effective means of controlling this plant but will not eradicate it (Ernst and Ketner 2007). The removal of aboveground tissue via cutting or mowing is not an effective method to eradicate plants because of the persistent, underground tuberous roots. To successfully control populations of this plant mechanically, the tubers need to be removed, and any resprouts repeatedly cut back (Englberger 2009). Tubers can be found as deep as 1 m in soil; therefore, deep tillage is necessary to remove tubers. Burning likewise can control plants above ground, and plants will produce shorter shoots after regrowth, but this is not a viable long-term option for control.

Chemical control is a more effective long-term approach of managing corallita infestations. The chemical recommendation on Pohnpei is to use triclopyr (Garlon™ 4) (Englberger 2009). For small plants, or new introductions, entire plants are uprooted and burned. For larger and/or more established infestations, a foliar spray application of 0.2 kg ae ha^{-1} (0.178 lb ae ac^{-1}) triclopyr (0.4% Garlon 4) is suggested. Approximately 1 wk after treatment when plants have died back, the tubers are uprooted and removed to prevent regrowth. For isolated individuals, undiluted triclopyr is applied directly to cut stems: 1 ml (0.034 oz) for smaller plants and 3 to 5 ml for larger plants. Revisiting treated areas is always necessary to ensure that corallita plants do not regrow and that all the tubers have been uprooted and removed from the site.

Ernst and Ketner (2007) conducted chemical trials on St. Eustatius and reported that both 25% triclopyr (165 kg ae ha^{-1}) and 25% glyphosate (122 kg ae ha^{-1}) foliar spray applications at a total volume of 1,370 L ha^{-1} (362 gal ha^{-1}) and stump treatment (2 to 3 ml of undiluted herbicide) were very effective in preventing plant regrowth, with no plant regrowth 6 wk after treatment. In addition, glyphosate was most effective at killing underground tubers. All tubers from plots treated with foliar-applied glyphosate were nonviable. Although these herbicide trials were extremely effective in controlling corallita, they did involve very high rates and total spray volumes of these two herbicides, which might not be environmentally or economically acceptable if large areas require treatment.

Based on these studies, for corallita control, we recommend a combination of manual and chemical methods. For smaller infestations, whole plants should be removed and uprooted. Larger infestations can be controlled by first removing or burning the aboveground tissue. Three to four wk later, the regrowth can by sprayed with a foliar application of triclopyr (0.2 kg ae ha^{-1}). Any additional regrowth can be cut back manually, or another application of herbicide might be necessary to kill remaining plants. Glyphosate is another effective herbicide, but at the moment we lack sufficient trials to make a recommendation for foliar spray application rate that is effective yet environmentally responsible. For the time being, we recommend restricting the use of glyphosate to cut-stump treatment of 2 to 3 ml of undiluted herbicide applied to large individuals.

Discussion

Corallita is a common weed throughout the tropics, although not yet well-documented as such. This plant clearly has been introduced as an ornamental and now is becoming naturalized around the tropics, and needs to be controlled. When neglected, corallita can spread and persist through the development of underground tuberous roots. Local naturalization primarily is accomplished sexually through dispersal of achenes by water or asexually through the spread of tuberous roots in soil, although other undocumented means of dispersal are possible. For now, the best means of control is a combination of mechanical and chemical methods.

The extent of its distribution across the tropics is extreme. The vine occurs on islands with few inhabitants such as Agrihan (pop. 10), Ua Huka (pop. 550), and many other remote islands in the South Pacific (e.g., Guam, Tahiti, Yap). Islands also are regions where corallita poses the greatest threat to local biodiversity and ecosystem function and stability. The relative susceptibility of islands to invasion is well-documented (see Loope and Mueller-Dombois 1989 for review). Many of the islands where corallita is a problem are sites also colonized by other invasive species, notably the brown tree snake (*Boiga*

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irregularis Merrem) on Guam or the Indian mongoose (*Herpestes javanicus* E. Geoffroy Saint-Hilaire) in Hawaii. The problem posed by an intentionally-introduced ornamental underscores the need for island regulatory agencies to carefully screen for new introductions on their territories.

Although many of our most problematic weeds were introduced unintentionally, a substantial proportion of invasive plants have been introduced intentionally as ornamentals. We encourage regulatory agencies from tropical island nations to include corallita on their restricted plant lists to limit its introduction onto islands. Currently corallita does not pose a major threat in the United States, though it has been documented as naturalized in Alabama, Florida, Georgia, Hawaii, Louisiana, and Texas, and as a garden ornamental in six other western or southern states: Arizona, California, Mississippi, New Mexico, North Carolina, and South Carolina. Climate change over the next several decades undoubtedly will affect the geographic ranges of invasive species (Clements and DiTommaso 2011; Hellman et al. 2008). For example, *Pueraria lobata* (Willd.) Ohwi (kudzu), a leguminous vine largely restricted to the southern United States, already is spreading in Maryland, and has been documented as far north as Connecticut (Mitich 2000) and Massachusetts. Because of likely range expansion into colder climes, and the current abundance of corallita in tropical regions, we suggest close monitoring of any introduced individuals in temperate regions to prevent spread.

One clear conclusion from this review is the paucity of studies documenting the invasive properties of corallita and methods of control. Much of the knowledge of corallita as an invasive is anecdotal, and herbicide trials have been undertaken by land managers on relatively small areas. We call for further studies into the invasive biology of corallita, including determining the: (1) primary mode of dispersal, (2) response of seeds to saline conditions, (3) presence of herbivores, and (4) response of plants to larger scale herbicide trials. In particular, a better understanding of the dispersal mode for this species can be used to identify key vectors to target and control for other global invaders as well.

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Appendix 1. List of voucher specimens of corallita for documentation of nonnative spontaneous occurrence worldwide; naturalized or invasive specimens included, specimens in cultivation or from the native range excluded. At least one voucher is provided per locality, and the oldest voucher was chosen to document the earliest occurrence for known presence in a county/municipality or on an island. All species determinations were made by J. Burke. Herbarium specimens are from BH, F, MO, NY, P, TEX, and US (standardized herbarium acronyms are from Index Herbariorum, International Association for Plant Taxonomy, 1990).

NORTH AMERICA

United States. ALABAMA. Mobile Co.: South side of Mobile along highway, 22 Sep 1969, *Kral 37385* (US). **FLORIDA. Dade Co.:** Black Point Bridge, 27 Feb 1920, *Young 352* (BH). **Lee Co.:** Middle Captiva Island, 21 Dec 1972, *Brumbach 8143* (NY, US). **Monroe Co.:** Big Pine Key, 8 Sep 1980, *Brumbach 9731* (NY). **Orange Co.:** 24 Oct 1981, *D.S. & H.B. Correll 52930* (NY). **Pasco Co.:** Along C-41 0.5 mi E of junction with I-75, 10 Jun 1984, *Hansen 9949* (TEX). **GEORGIA. Dougherty Co.:** vacant lot near railroad station, Albany, 5 Aug 1947, *Thorne 5865* (BH). **HAWAII. Lanai**: 15 Aug 1963, *Degener et al. 28542* (NY). **Oahu:** Halekulani, 20 Feb 1920, *Marquand s.n.* (NY). **LOUISIANA. Terrebonne Parish:** Houma, 20 Sep 1936, *Arceneaux 190* (BH). **TEXAS. Cameron Co.:** near Brownsville, 1 Dec 1945, *Cory 51416* (NY). **Duval Co.:** 1 mi NE of Realitos, 30 May 1969, *Correll & Correll 37367* (TEX). **Harris Co.:** Houston, 3 Oct 1914, *Fisher 208* (US). **Kleberg Co.:** NE part of Naval Air Station Kingsville, 19 Jul 2006, *Carr 24936* (TEX). **Starr Co.:** 2.1 miles SW of southern jct. US Rt. 83 and F.M. 2098, 19 Apr 1994, *Carr 13597 and Elliott* (TEX). **Travis Co.:** near Austin, 27 Jul 1943, *Harpin & Waldorf 45* (NY). **Webb Co.:** 1100 block of San Dario St., Laredo, 25 Apr 1965, *Martinez & Cantu 5* (TEX).

CARIBBEAN

Antigua and Barbuda. ANTIGUA. Parham, 26 Aug 1937, *Box 995* (US).

Bahamas. CAT ISLAND. Near Dumfries, 22 Oct 1967, *Byrne 372* (NY). **CROOKED ISLAND.** Hills NE of Cabbage Hill, 22 Feb 1975, *Correll 44478* (F-2, NY). **CENTRAL ABACO.** Great Abaco, E side of Marsh Harbour, 16 Mar 1975, *Correll & Meyer 44716* (NY). **EXUMA.** Hummingbird Cay, near cistern, Mar 1978, *Blair 4799* (MO, US).

Cayman Islands (UK). GRAND CAYMAN ISLAND. Midland District, Bodden town, 2 Jun 1963, *Crosby 46* (TEX).

Cuba. CIENFUEGOS. Castillo de Jagua, 16 Sep 1895, *Combs 563* (F, MO, NY, US); Soledad, 3 Mar 1926, *Jack 4163* (US). **MAYABEQUE.** Canasi to Boca de Canasi, 18 Feb 1956, *Morton 10228* (US). **SANTIAGO DE CUBA.** Crucero de Firmeza, 9 Sep 1951, *Lopez 113* (US).

Dominica. ST. PETER. Between Coulibistri and Colihaut, 30 Jul 1964, *Wilbur et al. 8119* (F, MO, NY, TEX, US).

Dominican Republic. LA ROMANA. W side of Río Chavon, NW of Presa Chavon, 1.5 km N of La Romana–Presa Chavon road, 17 Nov 1980, *Mejia & Zanoni 9122* (MO, NY). **MONTE CRISTI.** Monción, *Valeur 255* (F, MO, NY, US). **PERAVIA.** Paso del Joba, 12 km NW of Bani, entry to La Monteria, 6 May 1981, *Mejia et al. 13237* (NY). **SANTO DOMINGO.** Ciudad Trujillo, 1 mi W of city, 4 Nov 1945, *Allard 13038* (US).

Guadeloupe (FRANCE). BASSE-TERRE ISLAND. Gourbeyre, 1892, *Duss 2182* (F, NY, US).

Haiti. NIPPES. Miragoane , 20 Sep 1927, *Eyerdam 543* (US). **NORD.** Chaine Bonnet Leveque, next to the Palacio Sans Souci en Milot, 19 Nov 1982, *Zanoni et al. 24475* (MO, NY). **NORD-OUEST.** Vicinity of Jean Rabel , 7 Feb 1929, *Leonard & Leonard 12753* (NY, US). **OUEST.** Plaine Cul-de-Sac, north bank of Lake Etang/Trou Caiman, 27 Jan 1984, *Zanoni et al. 28758* (NY).

Jamaica. Cornwall Co.: St. James Parish, Montego Bay, 28 Mar 1920, *Maxon & Killip 1660* (F, US); St. Elizabeth Parish, Balaclava, 11 Mar 1927, *Orcutt 696* (MO). **Middlesex Co.:** St. Catherine Parish, near Spanish Town, 30 Aug 1908, *Britton 3071* (NY). **Surrey Co.:** Kingston Parish, Causeway Bay near Kingston, Jan 1974, *Katsuro 54* (TEX), St. Andrew Parish, Halfway Tree, 27 Jul 1939, *Philipson 505* (NY), St. Thomas Parish, between Easington and Llandewy, 24 Nov 1963, *Proctor 24240* (TEX).

Montserrat (UK). Coconut Hill, 27 Jan 1907, *Shafer 716* (F, NY, US).

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Puerto Rico (US). Mpio. Bayamon: Santurce, 1899, *Goll 75* (US). **Mpio. Camuy:** Bo. Santiago, Rte. 488 next to Río Camuy, 2 Jul 1991, *Axelrod et al. 2594* (NY). **Mpio. Cataño:** Isla de Cabra, 29 Jul 1979, *Woodbury s.n.* (NY). **Mpio. Coamo:** near Coamo, 8 Feb 1929, *Britton & Britton 9213* (NY). **Mpio. Fajardo:** Seven Seas, carr. 987, 4 Apr 1987, *Ortiz & Davila 26* (NY). **Mpio. Guayanilla:** Along rte. 335, 5 km S of Yauco, 20 Jun 1991, *Miller et al. 6499* (MO). **Mpio. Vieques:** Isla de Vieques, Las Marias, 5 Feb 1914, *Shafer 2706* (NY, US).

Saint Barthélemy (France). Gustavia, 27 Nov 1937, *Questel 80* (NY).

Saint Eustatius (Netherlands). Oranjestad, 24 Jun 2009, *Burke 1-17* (BH).

Saint Kitts and Nevis. St. Kitts: Basseterre, 23 Aug 1932, *Johnson 1090* (NY).

Saint Vincent and the Grenadines. St. Vincent: near Kingstown, 10 May 1947, *Morton 5735* (US).

Trinidad and Tobago. TRINIDAD. Moruga, 19 Mar 1921, *Britton & Broadway 2452* (NY, US).

U.S. Virgin Islands. ST. CROIX. Diamond Ruby, 3 Dec 1925, *Thompson 1051* (NY). **ST. JOHN:** Caneel Bay, Dec 1940, *Woodworth 241* (F). **ST. THOMAS.** Villa Olga, 22 Sep 1962, *Croat 80* (MO).

SOUTH AMERICA

Brazil. BAHIA. 190 km S of São Paulo de Paraiso, 8 Feb 1985, *Gentry 49950* (MO). **PARA.** Belem, Mar 1929, *Dahlgren & Sella 402* (F, US). **RIO DE JANIERO.** Rio de Janiero, 20 Dec 1923, *Bailey & Bailey 267* (BH).

Colombia. ATLÁNTICO. Barranquilla, Puerto Colombia, 20 Apr 1974, *Plowman 3542* (US). **BOLÍVAR.** Santa Catalina, Loma Las Puas, via Arroyo Grande a Las Canoas, 4 Feb 1987, *Cuadros 3290* (MO). **CHOCÓ.** Quibdó, barrio Pan de Yuca, 24 Aug 1984, *Cordoba & Garcia 331* (MO). **CASANARE.** Orocue, Río Meta, 3 Nov 1933, *Cuatrecasas 4418* (F). **CUNDINAMARCA.** Poblado de Nariño, 15 Feb 1986, *Fernandez 5197 & Jaramillo* (MO). **MAGDALENA.** Río Manzanare, 29 Dec 1948, *Giacometto 1058* (US).

Ecuador. GALÁPAGOS. Santa Cruz Island, Graffer farm, 6 Mar 1960, *Leveque 33* (US).

Guayana. DEMERARA-MAHAIACA. Georgetown, S. Rumveldt Park, Houston Estate, 21 Sep 1986, *Pipoly et al. 8699* (NY, TEX, US). **MAHAICA-BERBICE.** Arbary River mouth and along canals, 28 Mar 1987, *Pipoly et al. 11254* (NY, TEX, US).

Peru. HUÁNUCO. Tingo Maria, frente a Tingo Maria, izquierda Río Huallaga, 10 Oct 1959, *Ferreyra 13861* (US). **LORETO.** Near Iquitos, 17 Jul 1929, *Williams 1529* (F). **SAN MARTÍN.** Tarapoto, 10 Dec 1929, *Wiliams 5949* (F).

Venezuela. AMAZONAS. 20 km S of confluence of Rio Negro and Brazo Casiquiare , 21 Apr 1979, *Liesner 6848* (MO). **ANZOÁTEGUI.** Independencia, Río Orinoco, alrededores de Corrientoso, Sep 2003, *Diaz 6535* (MO). **BOLÍVAR.** Ciudad Bolívar, 4 Nov 1929, *Holt & Gehriger 22* (US). **DELTA AMACURO.** Lower Orinoco, Sacupana, May 1896, *Rusby & Squires 35* (F, MO, NY-2, US-2). **FALCÓN.** Downtown Guamachito, 24 Jan 2007, *Luckow et al. 4630* (BH, VEN). **NUEVA ESPARTA.** Isla Margarita, El Valle, Aug 1901, *Miller & Johnson 53* (F, MO-2, NY, US). **MÉRIDA:** Mpio. La Punta: Dto. Liberator, a la La Parroquia, 14 Mar 1972, *López-Palacios 2763* (US). **MIRANDA.** San Jose de los Altos, 26 Nov 1984, *Fernandez 17* (MO). **MONAGAS.** Between La Toscana and Chaguaramal, 11 Mar 1967, *Pursell et al. 8847* (NY, US).

AFRICA

Cameroon. SOUTH PROVINCE. Near Bipindi, 15 Jan 1987, *Manning 1358* (MO).

Côte d'Ivore. Grand Lahou, sur le cordon lagunaire, 18 Oct 1986, *Gautier 505* (MO).

Equatorial Guinea. BIOCO. Malabo-Luba, 27 Jul 1986, *Carvalho 2110* (NY). **Madagascar. ANALANJIROFO.** Along rte. 5 from Fenerive [Fenoarivo] to Maroantseta , 28 Feb 1975, *Croat 32538* (MO). **ATSIMO-ANDREFANA.** 8-16 km E of Tulear [Toliara] on road to Tananarive [Antananarivo], 7 Feb 1975, *Croat 30983* (MO).

South Africa. LIMPOPO. Transvaal, Legalameetse Nat. Res., Paris, near house Scott Branch, 2 Apr 1985, *Stalmans 524* (MO).

Sudan. Khartoum, 26 Apr 1975, *D'Arcy 9155* (MO).

Tanzania. DAR ES SALAAM. Dar es Salaam, low sea cliffs along Kenyatta Dr., 21 Dec 1984, *Gereau 1546* (MO). **IRINGA.** Ludewa, Lake Nyasa shore up to Lupingu, 31 Jan 1991, *Gereau & Kayombo 3795* (MO).

ASIA

China. GUANGDONG. Guangzhou, vicinity of Canton, 4 Sep 1934, *Guo 80469* (MO).

Indonesia. JAVA. Ngadirejo [?], 1875, *Kuntze s.n.* (NY-2). **SUMATRA.** Air Joman, Asahan, E of Serbangan, Jul 1935, *Boeea 8253* (NY, US).

Philippines. LUZON ISLAND. Orion Province: Bataan, Nov 1914, *Merrill 3314* (NY, US).

Sri Lanka. EASTERN. East side of Valachchenai bridge, on hwy. A15, 20 Apr 1968, *Mueller-Dombois 680420-17* (US). **NORTH WESTERN.** 0.5 mi beyond Kalpitiya, 14 Nov 1970, *Fosberg & Jayasuria 52756* (MO, US).

Taiwan. Chiayi Hsien: Chuchi Hsiang, near Hsiangkuang Temple, 5 May 1994, *Lin 460* (MO). **Tainan Co.:** Matou, 23 Oct 1988, *Tateishi & Kajita 25015* (MO).

Thailand. CHIANG MAI. Chiang Mai, 4 Aug 2008, *Skema 436* (BH).

Vietnam. KON TUM. Dak Gley, 28 Nov 1995, *Averyanov VH2118* (MO).

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OCEANIA

Federated States of Micronesia.TRUK-MOEN. Nantaku, 20 Aug 1980, *Fosberg 60387* (US).

French Polynesia. LEEWARD ISLANDS. Maupiti, E coast, Maupiti village, 23 Aug 1985, *Fosberg 64926* (US). **MARQUESAS ISLANDS. Ua Huka:** village of Vaipaee, 30 Jun 1997, *Perlman 15867* (NY).

Guam. Sumay, 7 Apr 1936, *Bryan 1086* (NY, US), Pipeline Rd. in Chaot River Ravine, 26 Jun 1980, *Fosberg 59663* (US), Orote Peninsula, 18 Mar 1946, *Moore 331* (US), near Finaguayac, 29 Aug 1954, *Moran 4488* (US).

Kiribati. Betio Island: 9 Mar 1968, *Adair 132* (US).

Northern Mariana Islands (USA). Rota Mun.: Behind W dock, 16 May 1966, *Evans 1966* (NY, US). **Tinian Mun.:** Lake Hagoya, N end of island, 8 Jun 1946, *Fosberg 24794* (NY, US).

Palau. KOROR. Koror Island, 16 Dec 1966, *Blackburn E29* (US).

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