

# The role of habitat, landscape structure and residence time on plant species invasions in a neotropical landscape

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**Abstract:** Plant invasions in tropical agricultural landscapes have been poorly studied so far. Here, we use plot data collected in 2015 in the La Gamba valley in southern Costa Rica to analyse the spread of two invasive alien species (*Hydrilla verticillata*, *Hedychium coronarium*) on the landscape level. In total, we recorded the aquatic *H. verticillata*, which was locally introduced into the La Gamba valley in 2005, in 26% of all plots (size: 15 m<sup>2</sup>), while *H. coronarium*, which occurs along water courses, was recorded in 80% of all plots (size: 25 m<sup>2</sup>). Generalized Linear Models (GLMs) showed that the habitat type invaded and shading had no significant effect on *H. verticillata* presence and abundance. However, proximity to the point of local introduction and habitat diversity in the adjacent landscape did positively affect its presence. For *H. coronarium*, GLMs showed a significant correlation with the invaded habitat type. The probability of *H. coronarium* presence was highest in herbaceous vegetation and cover was higher compared with other habitats. There was no effect on native plant species richness and cover by *H. verticillata*, while *H. coronarium* exerted a negative impact on herbaceous plant species number and, in particular, cover. *Hydrilla verticillata* is a rather recent addition to the local alien flora, and thus dispersal limitation still restricts its local range. Compared with observed rates of spread in other regions, spread velocity within the first decade of its local presence was low. In contrast, *H. coronarium* has been locally present for a substantially longer time period. This species encounters suitable habitat conditions in herbaceous vegetation along water courses, where it builds up dense clonal stands which negatively affect herbaceous vegetation. Our results show that while both study species are invasive in Central American lowlands, their local abundance and impacts on native vegetation may differ profoundly.

**Key Words:** distribution, *Hedychium coronarium*, *Hydrilla verticillata*, habitats, impacts, invasions, spread

## INTRODUCTION

A rapidly increasing number of plant species has become established outside their native range due to human agency (Van Kleunen *et al.* 2015), and some of these exert negative impacts on the environment or socio-economy (Simberloff *et al.* 2013, Vilà *et al.* 2010, 2011). Despite intensive research, the factors that promote the spread of alien species and that modulate their impacts on native biota are insufficiently understood (Pyšek *et al.* 2008). In general, research has shown that the spread of alien species at the landscape scale is influenced by the interplay

of properties of the spreading species (Pyšek & Richardson 2007), the resident vegetation (e.g. functional traits of native species) (Carboni *et al.* 2016), ecosystem properties (e.g. disturbance regime, the spatial configuration of habitat patches) (Carboni *et al.* 2016, Milbau & Nijs 2004) and propagule pressure (Chytrý *et al.* 2008a, Colautti *et al.* 2006, Lockwood *et al.* 2005, Pyšek *et al.* 2009). This complex interaction of a suite of factors renders generalizations and predictions of biological invasions inherently difficult.

With the important exception of islands (Daehler 2006, Denslow *et al.* 2009, Kueffer *et al.* 2010), tropical ecosystems are so far less affected by biological invasions than temperate or subtropical regions (Van Kleunen *et al.* 2015). However, while there is little evidence of the

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spread of alien plant species into undisturbed rain forests (Fine 2002, Padmanaba & Corlett 2014; but see Dawson *et al.* 2009, Parthasarathy *et al.* 2012), evidence has accumulated that cultural landscapes and anthropogenic ecosystems can be heavily invaded in the tropics (Barbier 2007, Lopez 2012, Padmanaba & Corlett 2014). Similar to regions in cooler climates (Chytrý *et al.* 2008a), aquatic habitats and riverine habitats in the tropics are particularly affected by increasing levels of invasion (Richardson *et al.* 2007, Thomaz *et al.* 2008). This is attributed to three main factors: running water is an excellent conduit for the transport of propagules (Chytrý *et al.* 2008b, Richardson *et al.* 2007), these habitats have been strongly modified by humans, and frequent natural disturbances of riparian ecosystems facilitate alien species invasions (Chytrý *et al.* 2008b, Davis *et al.* 2000, Parendes & Jones 2000, Richardson *et al.* 2007).

So far, invasion processes at the landscape scale have only rarely been analysed in tropical regions. However, due to the progressive encroachment of agriculture into natural forests (Ellis *et al.* 2010, Wassenaar *et al.* 2007), the spread of alien species has gained momentum in many tropical regions (Dawson *et al.* 2009, Lopez 2012, Seebens *et al.* 2015). Consequently, understanding the spread of alien species in the tropics has become a priority for researchers and conservationists alike (Barbier 2007, Padmanaba & Corlett 2014).

Here, we focus on two alien plant species which have become invasive in a range of tropical regions: the aquatic *Hydrilla verticillata* (Langeland 1996) and *Hedychium coronarium* (Soares & Barreto 2008) which is invading riverine habitats. By using plot data from a cultural landscape – the La Gamba valley – in southern Costa Rica, we test the following hypotheses: (1) Short local residence time limits the current distribution of the study species and has led to a yet incomplete colonization of suitable habitat patches; (2) Ecosystem properties of the invaded habitat patch as well as landscape context modulate the frequency and abundance of the study species; and (3) The presence and abundance of the study species exert negative impacts on native plant species diversity and cover.

## METHODS

### Study region

The La Gamba valley is a lowland region (50–100 m asl) of *c.* 15 km<sup>2</sup> size in the Puntarenas district of Costa Rica in the Pacific Region close to the Golfo Dulce (8°4'61"N, 83°12'97"W). The climate is humid with annual average rainfall of *c.* 6000 mm and a short dry period from December to April. Mean temperature is 28.3°C (Weissenhofer *et al.* 2008). The La Gamba

valley, formerly covered with rain forest, was colonized and forests were largely cleared on the flat valley bottom and on gentle slopes from the 1950s onwards, when the United Fruit Company established banana plantations in the region, which were abandoned in the 1980s (Weissenhofer *et al.* 2008). Since then the dominant form of land-use has been agriculture, especially rice paddies and cattle pastures. Moreover, oil palm plantations have been established since the turn of the millennium (Höbinger *et al.* 2012). The area is sparsely populated, with about 500 people living in the village of La Gamba. The La Gamba valley is surrounded by steep hills which are covered by primary and secondary forests which are largely protected by the Piedras Blancas National Park (Weissenhofer *et al.* 2008).

### Study species

Both study species are major invasive alien species in several tropical regions, which cause substantial negative impacts on invaded habitats (Langeland 1996, Soares & Barreto 2008). In the study region, both species belong to the most widespread herbaceous alien plant species in and along water bodies (W. Huber unpubl. data).

*Hydrilla verticillata* (L. f.) Royle (Hydrocharitaceae) is a submerged rooted water plant that forms dense mats under favourable conditions. Leaves are organized in whorls of 3–8, branching occurs only close to the water surface. Reproduction and spread is achieved by asexual (tuber-formation, stolons, fragmentation) and sexual reproduction. Colonization of new sites predominantly occurs via dispersal of plant fragments or propagules by running water, boats, contaminated soil and water fowl (Langeland 1996). Although the location and extent of the native range is uncertain, it likely encompasses tropical Asia, Africa and possibly northern Australia (Acevedo-Rodríguez & Strong 2012, Thomaz *et al.* 2008). Due to human-mediated spread, *H. verticillata* has become a pantropical species. It was introduced into the La Gamba valley at the Tropical Research Station of La Gamba as an ornamental plant in 2005 during the construction of a new pond (W. Huber unpubl. data). The prime example of the rapid invasive spread of *H. verticillata* is Florida, where it was discovered in 1960 and by 1988 it had colonized almost every water body (Langeland 1996). Presumably, its rapid spread was assisted by motorboats and waterfowl. In Florida, it causes severe impacts on native species composition in aquatic habitats by shading. For Costa Rica, no data on impacts caused by *H. verticillata* are available (E. Chacon unpubl. data). In different parts of its alien range, various means of management have been tested and carried out. However, *H. verticillata* is difficult to manage *inter alia* due to its high capacity of asexual reproduction (Langeland 1996).

*Hedychium coronarium* Koenig (Zingiberaceae) is native to lower altitudes of the eastern Himalayas (Nepal, India) (van Valkenburg & Bunyaphatsara 2001). This herb has white flowers, large leaves up to 60 cm long, and it reaches heights of up to 2.5 m. It has fleshy perennial rhizomes that are strongly aromatic, and as several culms can arise from the rhizome it is able to form dense clonal stands. *Hedychium coronarium* prefers shaded or semi-shaded ecosystems, tolerates flooding and waterlogged soils, and thus predominantly invades riverine ecosystems (Soares & Barreto 2008). Running water is also important for the dispersal of rhizomes and seeds and thus responsible for the spread along river and stream networks (Soares & Barreto 2008). *Hedychium coronarium* has become established in many tropical and subtropical regions worldwide, it is widespread in Costa Rica (Chacón & Saborío 2006, Huber *et al.* 2008) and considered invasive in neighbouring Panama (Hertentains *et al.* 1993, Lopez 2012). In Brazil, *H. coronarium* is invasive and management was implemented there to contain the spread of the species, but with limited success (Soares & Barreto 2008).

#### Data collection

Field data in the La Gamba valley were collected in February 2015 (data are available upon request from the corresponding author). For both study species, we established plots of standardized size, collected a similar set of explanatory variables, and recorded the geographic coordinates with a GPS.

For *H. verticillata*, we searched all potential parts of the study area, i.e. flat terrain in the valley bottoms where standing or slowly flowing water bodies do occur. When a potentially suitable water body was found, a plot of standardized size (15 m<sup>2</sup>) was established. When several water bodies occurred in close proximity (distance between ponds <50 m, which was the case in some rice paddies), only one plot was established. Within each plot, we recorded *H. verticillata* cover, cover of each resident plant species, and total cover of the resident vegetation. Plant cover was estimated in %. Nomenclature and taxonomy follows the Manual de Plantas de Costa Rica (INBio 1998). In addition, a range of environmental site conditions was collected: habitat type (forest, shrubland, herbaceous vegetation, other), degree of shading, connectivity (i.e. number of inflows/outflows), water body size (m<sup>2</sup>) and maximum water depth (cm), adjacent habitat diversity (i.e. number of habitat types in a radius of 50 m), and distance (m) to the point of local introduction (i.e. the Tropical Research Station La Gamba). In addition, in plots where *H. verticillata* was present, two subplots (5 m<sup>2</sup>) were established to analyse if differences in the abundance of *H. verticillata* within

the plot affected native species diversity and abundance. One subplot represents the section of the plot that was most invaded by *H. verticillata* (subplots invaded), whereas the other represents the section where the species was least abundant or absent (subplots uninvaded). In each subplot, we recorded the cover of *H. verticillata* and of the resident species.

For *H. coronarium*, we surveyed systematically the running water body network in the study region which consists of the Rio Bonito and its tributaries. We set the minimum distance between plots at 500 m to eliminate spatial auto-correlation. To select sites for study plots, we searched river sections of 100 m length for *H. coronarium* occurrence. When the study species was present, a plot of standardized size (25 m<sup>2</sup>) was established within these populations, otherwise a plot was selected at a non-invaded site. The following parameters were recorded: the size of the stream or river (breadth), the type of the river bank (i.e. steep, often eroded slopes vs. moderately steep slopes where sediments accumulate), habitat type invaded (herbaceous vegetation, shrubland, forests, other), and adjacent habitat diversity (number of habitat types in a radius of 50 m). In every plot with presence of *H. coronarium*, two subplots (5 m<sup>2</sup>) were established which represent the most (subplots invaded) and the least invaded (subplots uninvaded) section of the plot. In each subplot, we recorded cover of *H. coronarium* and number and cover of other resident herbaceous and woody plant species.

#### Data analyses

To test for the factors that influence the current distribution and abundance of the study species, we used Generalised Linear Models (GLMs) which included within-plot and landscape-context as explanatory variables. For *H. verticillata*, we included distance to the point of local introduction, habitat, adjacent habitat diversity, connectivity, depth and size of the water body, and degree of shading as explanatory variables. We fitted two GLMs, one from the binomial family with presence/absence of *H. verticillata* being the dependent variable, and one from the Poisson family with plant species cover of *H. verticillata* being the dependent variable (Faraway 2006). To test for species-co-occurrence of *H. verticillata* with the four most frequent native plant species in the plots (*Heteranthera reniformis*, *Limnocharis flava*, *Leersia hexandra*, *Eleocharis elegans*) we used Spearman's rank correlation analysis of species cover values.

For *H. coronarium*, we included habitat type (in the plot), adjacent habitat diversity, water course width and slope type as explanatory variables. Again, we fitted a binomial GLM with *H. coronarium* presence being the response variable and a GLM from the Poisson family

**Table 1.** Results of the Generalized Linear Models (GLMs) of the factors that influence the occurrence (presence/absence) of *Hydrilla verticillata* in the plots (n = 58) in the La Gamba Valley, Costa Rica. The explained deviance by the full model is 50.8%. Df, Deviance: the change in the degrees of freedom and the deviance respectively when dropping the respective variable from the full model.

	Df	Deviance	AIC	P-value
Null Model		39.54	55.54	
Distance to point of introduction	1	43.35	57.35	0.05
Habitat	4	47.32	55.32	0.10
Water body depth	1	42.88	56.88	0.07
Shading	1	41.34	55.34	0.18
Adjacent habitat diversity	1	49.41	63.41	0.002

with *H. coronarium* cover being the dependent variable. Further, we used GLMs from the Gaussian family to test if there was a correlation between *H. coronarium* cover and the number and cover of co-occurring woody and herbaceous species.

To see how different habitat types (herbaceous vegetation, shrubland, forest, other) were affected with respect to *H. coronarium* cover and differ from each other, an Analysis of Variance (ANOVA), together with a post hoc Tukey test, was conducted. All statistical analyses were done with the statistical software R using several contributed packages (nlme, mass, minqa, nloptr, sandwich, splines).

## RESULTS

### Distribution and abundance

In total, we recorded *H. verticillata* in 15 of 58 plots (Figure 1a). Mean cover of *H. verticillata* in the invaded plots was 61%, with a maximum cover of 98% in two plots. A decade after its introduction into the La Gamba valley, the occurrence probability of *H. verticillata* was positively correlated with proximity to the point of introduction (Table 1, Figure 2).

We recorded *H. coronarium* in 45 of a total of 56 plots (Figure 1b). Mean cover of *H. coronarium* was 35%, maximum cover was 90%. Results of an Analysis of Variance (ANOVA) showed that plots in herbaceous vegetation had significantly higher cover of *H. coronarium* than those located in woody vegetation types (Figure 3).

### Species co-occurrence and species diversity in plots invaded by *Hydrilla verticillata*

The resident vegetation in the *H. verticillata* plots was dominated by a few species. The four most abundant

**Table 2.** Results of the Generalized Linear Models (GLMs) of the factors that influence the cover of *Hydrilla verticillata* in the plots (n = 58) in the La Gamba Valley, Costa Rica. The explained deviance by the full model is 82.5%. Df, Deviance: the change in the degrees of freedom and the deviance respectively when dropping the respective variable from the full model.

	Df	Deviance	AIC	P-value
Null Model		15.65		
Distance to point of introduction	1	16.72	2.81	0.09
Habitat	4	20.36	12.41	0.01
Water body depth	1	17.51	4.89	0.02
Shading	1	16.66	2.67	0.10
Adjacent habitat diversity	1	20.41	12.54	<0.001

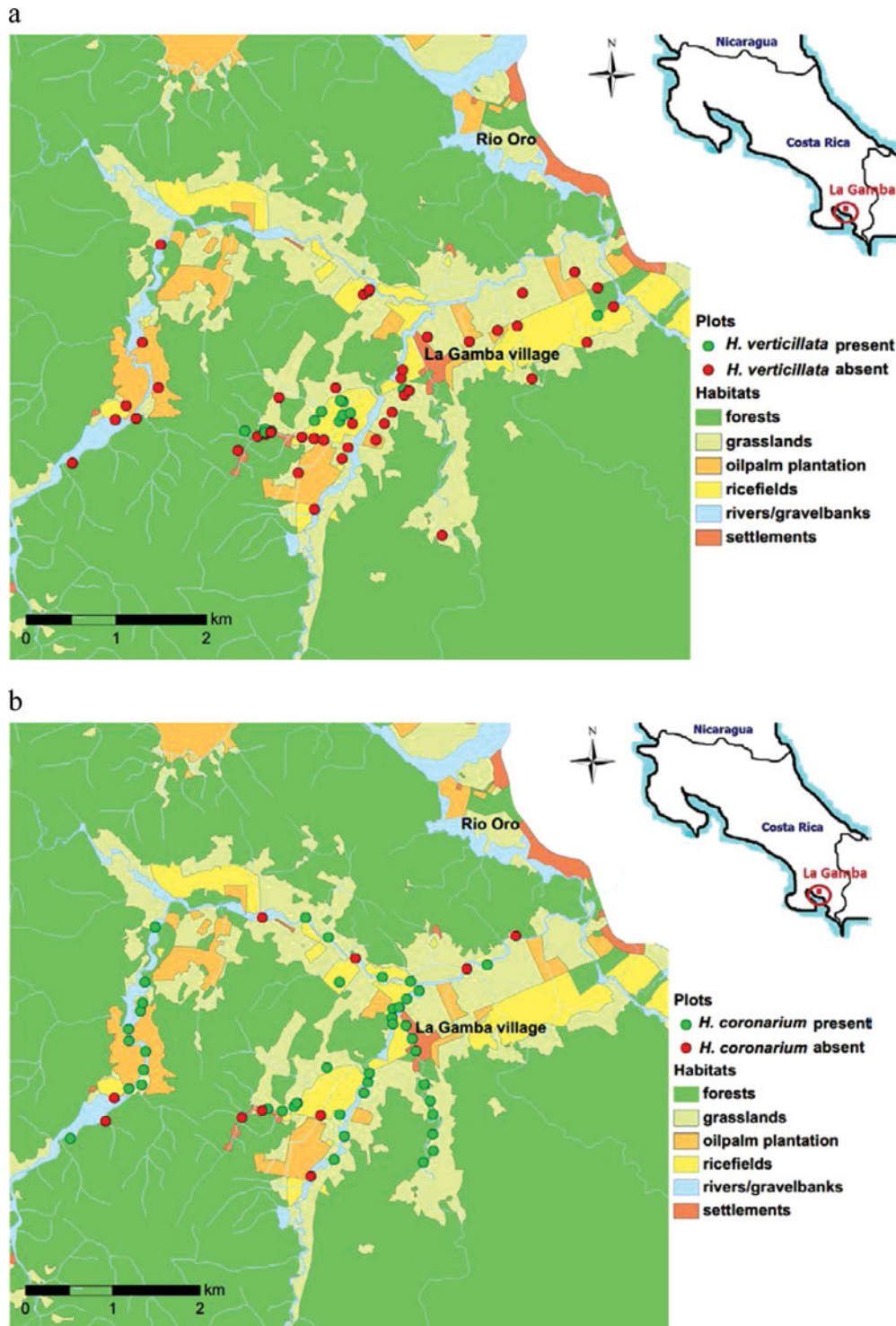
species in the plots were *Limnocharis flava* (recorded 31 times, 13 times accompanying *H. verticillata*), *Eleocharis elegans* (recorded nine times, twice accompanying *H. verticillata*), *Heteranthera reniformis* (recorded 29 times, 11 times accompanying *H. verticillata*), *Leersia hexandra* (recorded 31 times, seven times accompanying *H. verticillata*). The results of the Spearman's rank correlation analysis showed that there is a significantly positive correlation between the species cover of *H. verticillata* with *Heteranthera reniformis* ( $\rho = 0.31$ ,  $P = 0.02$ ), while the correlations were not significant for the other species: *Limnocharis flava* ( $\rho = 0.15$ ,  $P = 0.25$ ), *Eleocharis elegans* ( $\rho = -0.06$ ,  $P = 0.64$ ) and *Leersia hexandra* ( $\rho = -0.14$ ,  $P = 0.29$ ).

### Factors affecting the current distribution of the study species

The GLM showed that the habitat type invaded, i.e. backwater, pond, ditch and vehicle track, had no significant effect on *H. verticillata* presence (Table 1). Also shading of the plot did not influence the distribution significantly. Shallow water bodies were somewhat more likely to be invaded by *H. verticillata*, although the effect was not significant ( $P = 0.07$ ). However, distance to the point of introduction was significant ( $P = 0.05$ ). In addition, habitat diversity in the adjacent landscape did significantly affect *H. verticillata* presence. The relationship was positive, i.e. plots located in more diverse landscapes were more likely to be invaded. Further, the GLM using *H. verticillata* cover as response variable (Table 2) yielded only moderately different results.

For *H. coronarium* presence and cover, we found a significant correlation with the invaded habitat type (Tables 3, 4). The probability of *H. coronarium* presence was significantly higher in herbaceous vegetation



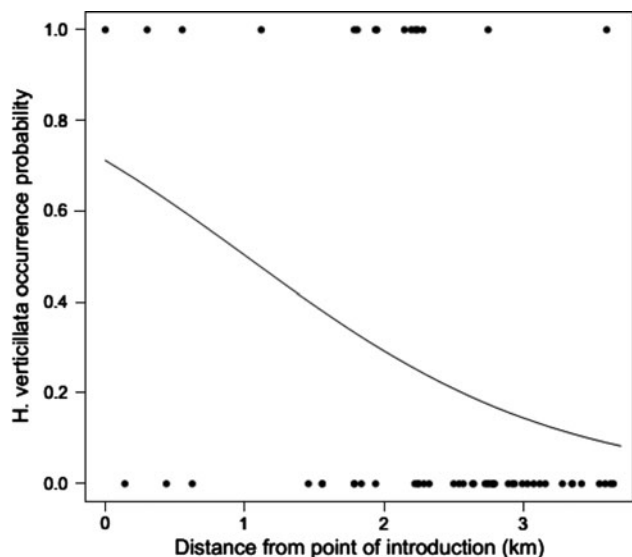


**Figure 1.** Location of the plots of *Hydrilla verticillata* ( $n = 58$ ) (a) and *Hedychium coronarium* ( $n = 56$ ) (b) in the study region (= La Gamba valley). Also shown are major habitat types, and the river and stream network. The inserts show the location of the study region in Costa Rica.

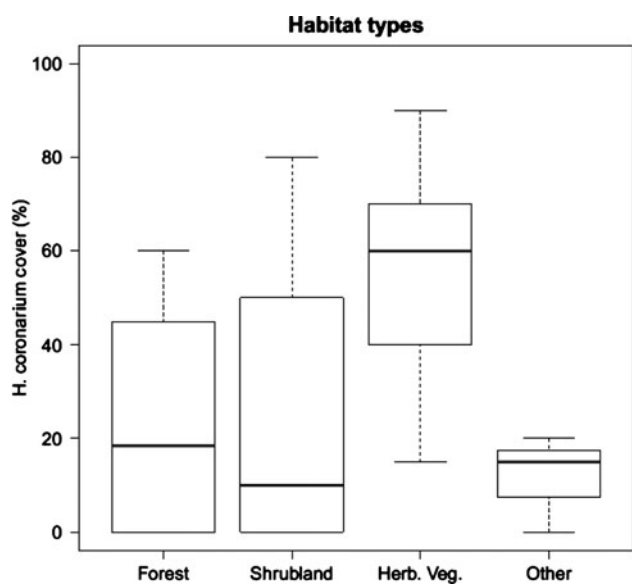
compared with other habitats. However, all other factors (river breadth, river bank slope, adjacent habitat types) included in the GLM did not influence *H. coronarium* presence and cover.

### Impacts on resident species

For both study species, we analysed the impact on native species richness and cover by comparing the subplots with



**Figure 2.** The influence of distance to the Tropical Research Station La Gamba (= the point of introduction of *Hydrilla verticillata* into the study region in 2005) on *H. verticillata* occurrence probability in plots (n = 58).



**Figure 3.** Average cover of *Hedychium coronarium* in the 56 study plots (forest: n = 8; shrubland: n = 26; herb. veg: n = 18; other: n = 4) located in different habitats in the La Gamba Valley, Costa Rica. Cover of *H. coronarium* in plots located in herbaceous vegetation is significantly higher than in other habitats (ANOVA; herb vs. forest: P = 0.035; herb vs. shrubland: P = 0.007; herb vs. other: P = 0.028).

high and low cover of the study species by GLMs. For *H. verticillata*, we found no effect on native plant species cover (correlation of fixed effects = 0.75). Similarly, there were no significant differences in woody species numbers or cover in the herb layer in invaded and

**Table 3.** Results of Generalized Linear Models (GLMs) of the factors that influence the occurrence (presence/absence) of *Hedychium coronarium* in 56 plots in the La Gamba Valley, Costa Rica. The explained deviance by the full model is 26%. Df, Deviance: the change in the degrees of freedom and the deviance respectively when dropping the respective variable from the full model.

	Df	Deviance	AIC	P-value
Null Model		6.54	72.64	
River breadth	1	6.70	72.02	0.24
Slope type	2	6.61	69.30	0.71
Habitat	3	7.87	77.04	0.02
Adjacent habitat diversity	9	7.53	62.56	0.54

**Table 4.** Results of Generalized Linear Models (GLMs) of the factors that influence the cover of *Hedychium coronarium* in 56 plots in the La Gamba Valley, Costa Rica. The explained deviance by the full model is 31.8%. Df, Deviance: the change in the degrees of freedom and the deviance respectively when dropping the respective variable from the full model.

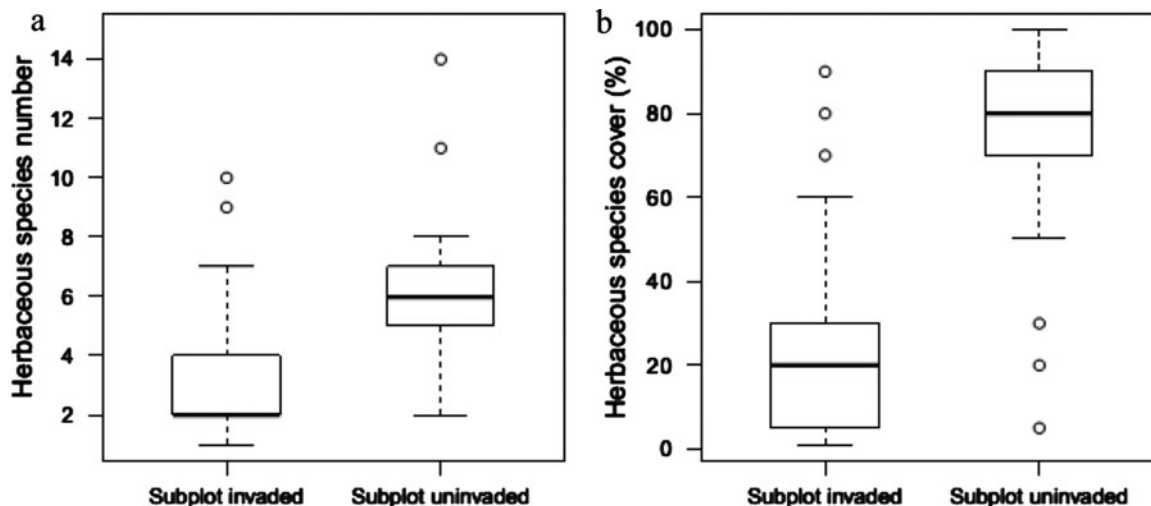
	Df	Deviance	AIC	P-value
Null Model		1183.1		
River breadth	1	1192.9	0.38	0.53
Slope type	2	1191.9	0.34	0.84
Habitat	3	1538.0	13.80	0.003
Adjacent habitat diversity	9	1381.1	7.69	0.56

non-invaded subplots of *H. coronarium*. However, we found a pronounced difference in herbaceous plant species number and, in particular, cover (Figure 4). *Hedychium coronarium* cover and the cover of co-occurring native species are significantly negatively correlated.

## DISCUSSION

### Invasion history, pattern and velocity of spread

The invasion history of *H. verticillata* in the La Gamba valley is unusually well documented due to the fact that the location (Tropical Research Station La Gamba) and timing (2005) of its regional first introduction are well-known (W. Huber unpubl. data). After a decade of spread, we found a positive correlation between *H. verticillata* presence and distance to the point of introduction (Table 1). This finding suggests that the spread of this species – most likely via the dispersal of plant fragments and propagules by running water, contaminated soil and water fowl – is still on-going in the La Gamba valley, and that dispersal limitation has yet precluded the colonization of more distant sites. Compared with observed rates of spread in other places of the world (Balciunas *et al.* 2002, Madeira *et al.* 2000), spread velocity within the first decade of the regional presence of *H. verticillata* was rather low. With the exception of one



**Figure 4.** Herbaceous plant species number (a) and cover (b) of subplots with high (subplot\_invaded) and low cover (subplot\_uninvaded) of *Hedychium coronarium* in the La Gamba Valley, Costa Rica. *t*-tests showed that differences in herbaceous plant species numbers were not significant ( $P = 0.55$ ), while differences in species cover were significant ( $P = 0.01$ ).

population, *H. verticillata* was still limited to sites within 3 km of the initial point of introduction. We argue that this low rate of spread results from the fact that suitable sites are small and isolated ponds, thus *H. verticillata* populations are small, the resulting propagule pressure is low, and colonization of new sites is difficult because of the isolated distribution of the ponds.

The local introduction history of *H. coronarium* is less well-documented, but it is known that it was already widespread in the study region in the mid-1990s (W. Huber unpubl. data), when botanical exploration of the study region commenced. Arguably, the species has been locally present for several decades, and thus likely has been able to colonize all or most suitable sites in the meantime.

### The role of habitat and landscape characteristics

We found a significant influence of adjacent landscape structure on the distribution of *H. verticillata*. Greater numbers of adjacent habitat types increased the probability of *H. verticillata* presence. This corroborates other studies which have shown that landscape variability facilitates invasion, e.g. by increasing the likelihood of occurrence of nearby suitable habitats or corridors for spread (Bennie *et al.* 2013, King & With 2002). But we note that our result has to be interpreted in the context of the landscape structure in the La Gamba valley. Plots which showed a low diversity in adjacent habitats were mostly located in ponds and ditches within extensive oil palm plantations (cf. Hübinger *et al.* 2012) and secondary forests. These habitats seem to be largely

unsuitable for *H. verticillata* due to dense shading. In contrast, more complex open landscapes (rice paddies, pastures, settlements) likely offered suitable habitats and thus fostered the spread of *H. verticillata*. In addition, agricultural machinery as used in harvesting rice is an effective device for the transport of propagules (Benvenuti 2007), and thus facilitates spread. Running water also plays an important role as a conduit for propagules and for asexual spread of *H. verticillata* (Dar *et al.* 2015, Le Maitre *et al.* 2014).

Of the factors included in the GLMs of *H. coronarium* presence and cover, only the invaded habitat type was significant (Tables 3, 4). *Hedychium coronarium* cover was significantly higher in plots located in herbaceous vegetation, likely because higher light availability than in forests or shrublands allowed *H. coronarium* to build up dense clonal stands. Other factors such as size of the river or the landscape context did not affect the presence and cover of *H. coronarium*.

### Evidence of impacts on native plant species

Both study species are known to exert substantial impacts on native species composition in neotropical regions (Langeland 1996, Soares & Barreto 2008, Thomaz *et al.* 2008). Surprisingly, we found no evidence of impacts of *H. verticillata*. Due to the absence of natural standing waters, *H. verticillata* only occurred in highly disturbed, anthropogenic water bodies. Plant species composition was similar in all plots where *H. verticillata* occurred as well as in potentially suitable, but yet not colonized, plots. This lack of evidence of negative impact may be

explained by the fact that few native pioneer species (e.g. *Heteranthera reniformes*, *Leersia hexandra*, *Limnocharis flava*, *Eleocharis elegans*) can cope with the disturbance-prone habitats. The absence of negative correlations between species cover values of *H. verticillata* and the four most abundant native species indicates that these species prefer the same habitat conditions but interspecific competition seems to be of limited importance, likely because of frequent disturbance events.

For *H. coronarium*, we documented negative impacts on native herbaceous plant species cover (Figure 4). Shading of dense clonal stands of the study species suppresses native herbaceous species, a fact that has also been reported from other tropical regions (Soares & Barreto 2008). In contrast, the number and cover of woody species in the plots were not negatively affected by *H. coronarium*. This finding is most likely related to the fact that woody species are released from shading once they have overgrown *H. coronarium*. In addition, long-lived woody species might have been present in the plots before they were invaded by the study species. However, we argue that negative impacts on woody species might emerge over time, as *H. coronarium* likely inhibits the germination of woody plant seedlings as has been proven for the closely related *Hedychium gardnerianum* (Minden *et al.* 2010a, b).

## CONCLUSIONS

While both species are major alien species in tropical regions worldwide, their local abundance and impacts on native vegetation differ profoundly. *Hydrilla verticillata* is a rather recent alien species in the study region, and thus dispersal limitation still restricts its local range. In addition, the scarcity of suitable habitats seems to contribute to a slow spread velocity which is in stark contrast to the rapid expansion of this species in other tropical regions (Langeland 1996). *Hedychium coronarium* has been present in the study region for a substantially longer time period, and we found no indication of ongoing spread on the landscape level. This species encounters suitable habitat conditions in particular in herbaceous vegetation along rivers and streams in the cultural landscape of the La Gamba valley, where it is able to build up dense clonal stands which negatively affect the cover of the native herbaceous vegetation.

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