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# Oecologia

## Topography shapes the local coexistence of tree species within species complexes of Neotropical forests --Manuscript Draft--

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<b>Abstract:</b>	<p>Forest inventories in Amazonia include around 5,000 described tree species belonging to more than 800 genera. Numerous species-rich genera share genetic variation among species because of recent speciation and/or recurrent hybridisation, forming species complexes. Despite the key role that tree species complexes play in understanding Neotropical diversification, and their need to exploit a diversity of niches, little is known about the mechanisms that allow local coexistence of tree species complexes and their species in sympatry. In this study, we explored the fine-scale distribution of five tree species complexes and 22 species within these complexes. Combining forest inventories, botanical determination, and LiDAR-derived topographic data over 120ha of permanent plots in French Guiana, we used a Bayesian modelling framework to test the role of fine-scale topographic wetness and tree neighbourhood on the occurrence of species complexes and the relative distribution of species within complexes. Species complexes of Neotropical trees were widely spread across the topographic wetness gradient at the local scale. Species within complexes showed pervasive niche differentiation along topographic wetness and competition gradients. Similar patterns of species-specific habitat preferences were observed within several species complexes: species more tolerant to competition for resources grow in drier and less fertile plateaus and slopes. If supported by partial reproductive isolation of species and adaptive introgression at the species complex level, our results suggest that both species-specific habitat specialisation within species complexes and the broad ecological distribution of species complexes might explain the success of these species complexes at the regional scale.</p>	

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Avril 7, 2020

**Object:** Submission of a manuscript to *Oecologia*

Dear Editor,

We would like to submit an original research article entitled "Topography shapes the local coexistence of tree species within species complexes of Neotropical forests" for consideration to publish in *Oecologia*. In this manuscript, we present an original research addressing the effect of topography on the distribution of species complexes and the local coexistence of species within species complexes based on a large inventories of 22 species within 5 species complexes associated to fine-scale topographic and neighbor crowding data.

Lowland Amazonia includes numerous species-rich tree genera sharing a large amount of genetic variation either because of recent common ancestry and/or recurrent hybridization, forming species complexes. Despite the key role that species complexes play in understanding Neotropical diversification, and the need for exploiting a diversity of niches for species complexes to thrive, little is known about local coexistence of Neotropical species complexes in sympatry. Combining full forest inventories, high-quality botanical determination, and LiDAR-derived topographic data over 120ha of permanent plots, we used a Bayesian modelling framework to test the role of fine-scale topography and tree neighbourhood on the presence of species complexes and the relative distribution of species within complexes. Species complexes of Neotropical trees were widely spread across topography at the local-scale, while species within species complexes showed pervasive niche differentiation along topographic position, water accumulation, and competition gradients. Our results suggest that both habitat specialisation of species within species complexes and the broad ecological distribution of species complexes might explain the success of these Neotropical species complexes at the regional scale

We believe that this manuscript would be a valuable contribution to *Oecologia* and attract a large readership as our results contribute to shed some light on species coexistence within the understudied Neotropical species complexes.

We have no conflicts of interest to disclose.

Thank you for your consideration.

Sincerely,

Sylvain Schmitt,  
on behalf of the co-authors

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# Topography shapes the local coexistence of tree species within species complexes of Neotropical forests

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## Authors' contributions

NT and SS conceived the ideas; SS, BH, and NT designed methodology; SS and BH analysed model outputs; SS, NT and MH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## **Abstract**

Forest inventories in Amazonia include around 5,000 described tree species belonging to more than 800 genera. Numerous species-rich genera share genetic variation among species because of recent speciation and/or recurrent hybridisation, forming species complexes. Despite the key role that tree species complexes play in understanding Neotropical diversification, and their need to exploit a diversity of niches, little is known about the mechanisms that allow local coexistence of tree species complexes and their species in sympatry. In this study, we explored the fine-scale distribution of five tree species complexes and 22 species within these complexes. Combining forest inventories, botanical determination, and LiDAR-derived topographic data over 120ha of permanent plots in French Guiana, we used a Bayesian modelling framework to test the role of fine-scale topographic wetness and tree neighbourhood on the occurrence of species complexes and the relative distribution of species within complexes. Species complexes of Neotropical trees were widely spread across the topographic wetness gradient at the local scale. Species within complexes showed pervasive niche differentiation along topographic wetness and competition gradients. Similar patterns of species-specific habitat preferences were observed within several species complexes: species more tolerant to competition for resources grow in drier and less fertile plateaus and slopes. If supported by partial reproductive isolation of species and adaptive introgression at the species complex level, our results suggest that both species-specific habitat specialisation within species

complexes and the broad ecological distribution of species complexes might explain the success of these species complexes at the regional scale.

## **Keywords**

species distribution; syngameon; habitat specialisation; Paracou

## **Introduction**

Tropical forests shelter the highest level of biodiversity worldwide (Gaston 2000), as already showcased by Connell (1978). Lowland Amazonian forest inventory plots include around 5,000 identified tree species belonging to 810 genera (ter Steege et al. 2013); thus many genera are species-rich. To understand the processes leading to such diversity, it is pivotal to understand what ecological mechanisms lead to the relative success of these species-rich genera. Among them, many have been shown to have a higher level of genetic polymorphism than species-poor genera, oftentimes sharing haplotypes among species, which is likely related to introgression among congeneric species (Caron et al. 2019). Indeed, interspecific hybrids occur in 16% of plant genera, and more often so in species-rich genera (Whitney et al. 2010).

Species that are morphologically similar, or have blurry morphological differences, and/or share large amounts of genetic variation due to recent common ancestry and/or hybridisation are defined as species complexes (Pernès and Lourd 1984; Brown et al 1995). Species complexes can result from adaptive radiation and segregation among species in the

use of environmental gradients, through a combination and reshuffling of genetic features among species in hybrid swarms (Seehausen 2004). These processes may multiply the number of potential ecological niches, in turn reducing competition among the species and helping the species gain reproductive isolation (Runemark et al. 2019). The establishment of a hybrid or derived species requires some degree of reproductive isolation from its progenitors to avoid becoming an evolutionary melting pot. Nevertheless, simulations suggest that low hybridisation success among congeneric species promotes the coexistence of species in the community by allowing for the persistence of rare species through hybridisation (Cannon and Lerdau 2015). Furthermore, the way we perceive the role of genetic connectivity among populations and species is quickly changing, as a growing body of literature supports that species-specific adaptations may be maintained or even maximised despite high levels of gene flow, especially if selective pressures are spatially and/or temporally variable (Tigano and Friesen 2016).

When closely related but distinct species that live in sympatry are connected by limited, but recurrent, interspecific gene flow, they are called a syngameon (Suarez-Gonzalez et al. 2018). Syngameons are particular in that they evolve responding to two contrasting evolutionary pressures, those acting at the species level maximizing species-level adaptations to a niche that reduces competition among species, and those acting at the syngameon level which benefit all constituent species. Syngameons as a whole might thus have a selective advantage, decreasing the overall risk of genus extinction, maximising population size, all the while allowing adaptation of their distinct species to specific niches and reducing competition among species (Cannon and Lerdau 2015). Consequently, and in



juxtaposition to other types of species complexes, syngameons are not necessarily a transitional or incipient phase of a process towards complete speciation but may be a highly successful evolutionary status *per se* (Cannon and Petit 2019). In one of the best known syngameons, the European white oak, the constituent species lack private cpDNA haplotypes indicating extensive hybridisation (Petit et al. 2002), but each of its constituent species includes unique portions of the genome that remain divergent (Hipp et al. 2019). Moreover, each species has unique ecological preferences, including drought and cold tolerance, and adaptation to alkaline soils (Leroy et al. 2019; Cannon and Petit 2019). The maintenance of the different species is orchestrated, in part, by the genes allowing their survival according to their ecological niche preferences (Leroy et al. 2019).

Similarly, Neotropical tree species show pervasive species-habitat associations (Fine et al. 2004; Esteves and Vicentini 2013). Specifically, congeneric species pairs may have contrasting preferences for topography and soil type (Itoh et al. 2003; Allié et al. 2015; Lan et al. 2016), and sometimes may grow in the same abiotic habitat but segregate according to light access (Yamasaki et al. 2013). Habitat specialisation may thus support congeneric species coexistence in sympatry. Among Neotropical congeneric tree species, many share genetic variation (Caron et al. 2019), which leads us to hypothesise that they may operate as syngameons.

Despite the key role of plant species complexes and syngameons in Neotropical ecology, diversification, and evolution (Pinheiro et al. 2018), little is known of the ecological drivers creating and maintaining diversity within Neotropical species complexes (Baraloto et al.

2012; Levi et al., 2019; ter Steege et al. 2013; Cannon and Petit 2019). Particularly, the generality of niche specialisation along environmental gradients among species within species complexes, as a potential driver of speciation and maintenance of species complexes, has not been addressed.

Here, we assessed the relative importance of the abiotic environment and biotic interactions in shaping species distribution within and among species complexes. We took advantage of the Paracou study site with more than 75,000 censused and geolocated individual trees in a highly diverse tropical forest site located in French Guiana, within the Guiana Shield in Amazonia. The Paracou site encompasses a diversity of micro-habitats through topographic variation ranging from seasonally flooded bottomlands to drier plateaus (Gourlet-Fleury et al. 2004) and displays variation in canopy gap size distribution (Goulamoussene 2016) and forest turn-over (Ferry et al. 2010). Combining tree inventories and LiDAR-derived topographic data, we used Bayesian modelling to address the following questions: (1) Are species complexes widely spread across biotic and abiotic environments, *i.e.* as generalists, or do they occupy specific niches, *i.e.* as specialists? (2) Do species within complexes also behave as generalists, *i.e.* do they occur throughout the environmental niche of species complexes, or does the biotic and abiotic environment favour niche differentiation within species complexes, *i.e.* do species within complexes have a narrower environmental niche than the complex? We considered as generalist those species whose variation in abundance does not imply a shift of species dominance along the environmental gradient, whereas we considered species as specialist those species whose variation in abundance implied a shift of species dominance along the gradient.

## **Material and Methods**

### **Study site**

The study was conducted in the northernmost part of the Guiana Plateau region, at the Paracou field station in French Guiana. The site is characterised by an average of 3,102 mm annual rainfall and a mean air temperature of 25.7 °C (Aguilos et al. 2018). Old tropical forest with an exceptional richness (*e.g.* over 750 woody species) develops in this area across a succession of small hills rising to 10–40 m a.s.l. (Gourlet-Fleury et al. 2004). A logging experiment was conducted in the Paracou station in 1986 (details in Hérault and Piponiot, 2018). We used seven undisturbed permanent inventory plots from Paracou (*i.e.*, six plots of 6.25 ha and one of 25 ha) which have been censused (*i.e.* diameter at breast height > 10 cm) every 1-2 years since 1984.

### **Species complexes**

The literature about syngameons is concentrated on temperate models (Levi et al. 2019b), and, to the best of our knowledge, no studies have inventoried species complexes in Amazonia or in the Paracou community (Pinheiro et al. 2018). From the Paracou database, we identified five species complexes based on evidence for low (phylo-)genetic resolution or plastid DNA sharing in the clade (Gonzalez et al. 2009; Baraloto et al. 2012; Caron et al. 2019): *Eschweilera* clade *Parvifolia* (Lecythidaceae; Chave et al. unpublished; Heuertz et al.

2020); *Licania* (Chrysobalanaceae; Bardon et al. 2016); *Iryanthera* (Myristicaceae); *Symphonia* (Clusiaceae; Torroba-Balmori et al. 2017); and *Talisia* (Sapindaceae). We removed species with less than ten individuals in Paracou in 2015, which resulted in five species complexes each including two to nine species (Table 1). The species in the five species complexes are dispersed by animals (*Eschweilera* see Prance and Mori 1993; *Iryanthera* see Howe 1983; *Licania* see Hammond et al. 1995, *Symphonia* see Forget et al. 2007; *Talisia* see Julliot 1996 and Théry and Larpin 1993). In addition, *Eschweilera*, *Licania*, and *Talisia* share haplotypes between species pairs (Caron et al. 2019) and *Symphonia* shows introgression between species pairs (Schmitt 2020), suggesting interspecific gene flow characteristic of syngameons. The Paracou community might include other species complexes. Nevertheless, our selection illustrates the phylogenetic diversity of species complexes in Paracou (see supplementary material S8), and the identified species complexes include species that are locally abundant and hyperdominant at the regional level (ter Steege et al. 2013), illustrating their significant ecological role in the Neotropics.

## **Environmental variables**

We consider the environment experienced by an individual to be composed of abiotic and biotic factors. We explored several topographic and biotic descriptors of Paracou plots (relative elevation, slope, curvature, topographic ruggedness index, topographic wetness index, elevation, canopy height and neighbourhood crowding index, see supplementary material S1). We chose topographic wetness index and neighbourhood crowding index as two little-correlated (Pearson's  $r = 0.12$ ) environmental descriptors to depict the

distribution of species complexes and that of species within complexes along the distribution of light, water, and nutrients.

The topographic wetness index (*TWI*), which was correlated to other topographic variables, identifies water accumulation areas and is thus critical for species distribution at local scale in tropical ecosystems (Ferry et al. 2010; Allié et al. 2015). *TWI* was derived from a 1-m resolution digital elevation model built based on data from a LiDAR campaign done in 2015 using SAGA-GIS (Conrad et al. 2015).

The neighbourhood crowding index (*NCI*; Uriarte et al. 2004), which was correlated to canopy height, was calculated from field censuses and used as a descriptor of the biotic interactions among trees. Although we recognise their potential non-negligible role in explaining species distributions, other biotic effects, such as variance in herbivory pressure and pathogen species richness, were not directly included into our analyses. The neighbourhood crowding index  $NCI_i$  for each tree individual  $i$  was calculated with the following formula:

$$NCI_i = \sum_{j|\delta_{i,j}<20m} DBH_j^2 \cdot \exp\left(-\frac{1}{4}\delta_{i,j}\right) \quad (1)$$

where  $DBH_j$  is the diameter of neighbouring tree  $j$  and  $\delta_{i,j}$  its distance to individual tree  $i$ .  $NCI_i$  is computed for neighbours at a distance  $\delta_{i,j}$  of up to 20m because *NCI* showed negligible effect beyond 20m in preliminary analysis. The size effect of neighbours was taken as their squared *DBH*, and hence proportional to their basal area. The distance effect

of neighbours was set to  $-1/4$ , corresponding to neighbours beyond 20m having less than 1% effect compared to the effect of neighbours at 0m.

## Analyses

### Distribution of complexes

The distribution of each species complex was inferred separately. We considered the occurrences of all individuals from species belonging to the species complex as presences, and all occurrences of trees belonging to other species as pseudo-absences. The presence of each species complex  $Presence_{species\ complex_k}$  was inferred with a logistic regression within a Bernoulli distribution (which corresponds to the best model form among several forms tested, see supplementary material S2 and S3):

$$Presence_{species\ complex_k} \sim Bernoulli[\text{logit}^{-1}(\alpha_k + \beta_k * X_k + \gamma_k * X_k^2)] \quad (2)$$

where  $X$  is the matrix of environmental descriptors ( $TWI$  and  $NCI$ ),  $\alpha$  is the intercept,  $\beta$  is a vector representing the slope of environmental descriptors and  $\gamma$  is a vector representing the quadratic form of effects of environmental descriptors for every species complex  $k$  (see supplementary material S9 and S10).

## Distribution of species

Joint distributions of species were inferred within each species complex. We used a softmax regression within a conjugated Dirichlet Process and Multinomial distribution to infer the distribution of species jointly and not independently:

$$Presence_{species_i|species\ complex_k} \sim Dirichlet\ Multinomial(\text{softmax}(\alpha_i + \beta_i * X_i + \gamma_i * X_i^2))(3)$$

where  $Presence_{species_i|species\ complex_k}$  represents the species  $i$  for every individual as a simplex of 0s and 1s (i.e. 0 for all other species from the species complex and 1 for the considered species),  $X$  is the matrix of environmental descriptors (i.e.  $TWI$  and  $NCI$ ),  $\alpha$  is the vector of species intercepts,  $\beta$  is a matrix representing the slope of environmental descriptors and  $\gamma$  is a matrix representing the quadratic form of effects of environmental descriptor for every species  $i$  of the species complex  $k$  (see supplementary material S9 and S10).

Environmental descriptors were all scaled to the unit in order to ease model inference and compare the strength of the effects among environmental descriptors. A Bayesian method was used to infer parameters of all models using stan language (Carpenter et al. 2017, see supplementary material S6 and S7) and the rstan package (Stan Development Team 2018) in the R environment (R Core Team 2020).

## Results

The topographic wetness index (*TWI*) and the neighbourhood crowding index (*NCI*) had null or weak effects on the probability of occurrence of species complexes, with the exception of an effect of *TWI* on the probability of occurrence of the *Eschweilera* clade *Parvifolia*, *Licania*, and *Iryanthera* (Fig. 1) species complexes. Wetter habitats (*TWI*>4) resulted in an increasing probability of occurrence of the species complex *Iryanthera* but a decreasing probability of occurrence of the species complexes *Licania* and *Eschweilera* clade *Parvifolia* (Fig. 1). However, the ranking of species complexes for probability of occurrence did not change significantly along the *TWI* gradient.

Conversely, the *TWI* strongly influenced the relative probability of occurrence of species within species complexes, with shifts in species dominance. The effect of the *NCI* was substantial, but did not shift species dominance within species complexes. For instance, the relative probability of occurrence of species *Iryanthera hostmanii*, *Eschweilera coriacea*, and *Symphonia globulifera* increased with water accumulation (*TWI*) while it decreased for *I. sagotiana*, *E. sagotiana*, and *S. sp1* (Fig. 2 and supplementary material S11). The change of relative probability of occurrence along the *TWI* gradient led to a shift of dominance among the aforementioned species within the *Symphonia*, *Eschweilera* clade *Parvifolia*, and *Iryanthera* species complexes, revealing a strong effect of topography. Similarly, the relative probability of occurrence of species *Licania membranacea*, *Eschweilera sagotiana*, and *Symphonia sp1* increased with neighbourhood crowding (*NCI*) while it decreased for *L. alba*, *E. coriacea*, and *S. globulifera* (Fig. 2 and supplementary material S11). Thus, two species



complexes, *Symphonia* and *Eschweilera* clade *Parvifolia*, included species with opposed preferences along environmental gradients defined through *TWI* and *NCI*. For instance, *S. sp1*, more tolerant to neighbourhood crowding (high *NCI*), grows preferentially in drier habitats such as plateaus (low *TWI*), while *S. globulifera* grows preferentially with decreased neighbourhood crowding (low *NCI*) and dominates in wet habitat such as bottomlands (high *TWI*).

## Discussion

Understanding the eco-evolutionary processes that underlie the origin and maintenance of species complexes, such as how species within species complexes exploit differential ecological niches (Runemark et al. 2019), is paramount to further our knowledge of Neotropical diversification processes (Pinheiro et al. 2018). Nevertheless, the ecological processes governing the distribution of species complexes in the Neotropics have received relatively little attention (Baraloto et al. 2012; ter Steege et al. 2013; Levi et al. 2019). Here, we show that species complexes of Neotropical trees span the full range of the studied topographic wetness and competition gradients, and are thus widely spread throughout light, water, and nutrient habitats at the fine spatial scale. Conversely, most species within species complexes show pervasive niche differentiation along topographic position, water accumulation, and competition gradients. Habitat preferences along topographic wetness and competition gradients were coordinated among species within several species complexes: species that are more tolerant to competition for resources grow in drier and less fertile plateaus and slopes, as opposed to wet and fertile bottom-lands, where species

that are less tolerant to competition for resources are more frequently found. Consequently, our results suggest that the ecologically broad distribution of species complexes combined with the habitat specialisation of species within species complex might explain the success of these Neotropical species complexes at the regional scale (ter Steege et al. 2013). This appreciation of the ecological abundance of species and their species complexes does not yet consider reproductive biology and interspecific gene flow. For this statement to hold more broadly, it is necessary to assume at least partial reproductive isolation of species and evolutionary adaptation of species to the fine-scale habitat structure, but with occasional adaptive introgression between species at the species complex level.

### **Species complexes are widely spread across habitats**

The general null or weak effects of our considered biotic and abiotic environmental variables on the abundance distribution of species complexes suggest that species complexes are widely spread throughout light, water, and nutrient gradients at the local scale, and that the species complexes thus behave as generalists that appear to benefit from the evolutionary advantages typical of generalists. Topographic wetness index (*TWI*) indicates the topographic position where water accumulates. Neighbourhood crowding index (*NCI*) represents competition with neighbours and thus access to light, water, and nutrients. *TWI* and *NCI* had no effect on the distribution of species complexes, at the exception of a weak effect of high *TWI* increasing the abundance of *Iryanthera*, and increasing the abundances of *Licania*, and *Eschweilera* clade *Parvifolia*. This results emphasises the generality of the widespread distribution of species complexes throughout

light, water, and nutrients gradients with either segregated species with ecological preferences or generalist species.

The higher abundance of the *Iryanthera* species complex in wet habitats has already been evidenced experimentally (Baraloto et al. 2007). Increased or decreased abundance of species complexes at high *TWI* values might be due to variations in species complex-specific adaptations to a more constraining habitat, for example anoxia in water-logged soils.

### **Species show pervasive niche differentiation within species complexes**

The repeated observation of species relative abundance variation within species complexes along biotic and abiotic environmental gradients represents evidence for pervasive niche differentiation of species within four locally abundant species complexes. Indeed, species within *Iryanthera*, *Licania*, *Symphonia*, and *Eschweilera* clade *Parvifolia* species complexes are segregated along a gradient from wet to drier habitats and a gradient from low to increased neighbourhood crowding.

Habitat segregation along topography and wetness gradients corresponds to the well-known bottomland to plateau gradient observed in Amazonia (Kraft et al. 2008; Ferry et al. 2010). Species within species complexes segregate between seasonally flooded habitats with frequent soil anoxia but increased soil fertility and drier uphill habitats with a higher risk of drought and reduced fertility, whereas few species grow preferentially in intermediate habitats (*e.g.* *Licania membranacea*, Fig. 2). Indeed, water-use strategies and

edaphic conditions are known to shape divergent habitat associations between congeneric species pairs (Baltzer et al. 2005). Our results are in agreement with previous evidence of species-habitat association with topography among sympatric congeneric species at local scale (Itoh et al. 2003; Allié et al. 2015; Lan et al. 2016; but see Baldeck et al. 2013b). We tested here topography in our study but not edaphic properties. Besides covariation with topography, edaphic properties have independent effects on the species distribution (Baldeck et al. 2013a), which may increase species niche differentiation within species complexes.

Species within species complexes segregate also between high neighbourhood crowding conditions that result in a decreased access to light, water, and nutrients and low neighbourhood crowding conditions where competition for resources is lower. Yamasaki et al. (2010) already evidenced segregation according to access to light between two congeneric species at local scale, but that grew in the same topography. In our study, *S. sp1*, *I. sagotiana*, *E. sagotiana*, and *T. hexaphylla* showed more tolerance to competition for resources (i.e. high *NCI*) and grow in drier and less fertile habitats (i.e. low *TWI*), whereas *S. globulifera*, *I. hostmannii*, and *E. coriacea* that grow in wet habitats also grow preferentially with less competition for resources. To the best of our knowledge, previous studies have shown segregation of species according to topography or light, independently but not together, which opens avenues for future studies on their joint effects.

## **Conclusion**

We found Neotropical tree species complexes to be widespread across habitats at local scale, while the species composing them showed pervasive habitat differentiation along topography and competition gradients. The pervasive niche differentiation among species within several species complexes might be related to parallel adaptation to local environment resulting in replicated functional strategies (Baraloto et al. 2007, Baltzer et al. 2005), with several diversification events across taxa (*e.g.* Fine et al. (2014) for *Protia*). Habitat specialisation reduces competition among the species and thus helps the species gain reproductive isolation for their establishment within species complexes (Runemark et al. 2019). Meanwhile, porous genomes allow for the transfer of adaptive genes through potentially rapid introgression (Cannon and Scher 2017) that may benefit one or several species, allowing for coevolution at the species complex level (Cannon and Lerda 2015). Consequently, if habitat specialisation allows at least partial reproductive isolation and if porous genomes allow adaptive introgression, our results suggest that both habitat specialisation of species within species complexes and the widespread distribution of species complexes might explain the success of these Neotropical species complexes at the regional scale (ter Steege et al. 2013).

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## **Conflict of interest**

The authors declare that they have no conflicts of interest.

## **Data accessibility**

TWI and spatial positions of individuals were extracted from the Paracou Station database, for which access is modulated by the scientific director of the station (<https://paracou.cirad.fr>).

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*Table 1: Identified species complexes with species including more than 10 individuals censused in the Paracou forest inventory. N represents the number of tree studied per species.*

Complex	Species	N
Iryanthera	<i>Iryanthera sagotiana</i>	381
Iryanthera	<i>Iryanthera hostmannii</i>	335
Licania	<i>Licania alba</i>	1117
Licania	<i>Licania membranacea</i>	442
Licania	<i>Licania canescens</i>	164
Licania	<i>Licania micrantha</i>	139
Licania	<i>Licania ovalifolia</i>	95
Licania	<i>Licania sprucei</i>	76
Licania	<i>Licania laxiflora</i>	37
Licania	<i>Licania parvifructa</i>	12
Licania	<i>Licania densiflora</i>	6
Parvifolia	<i>Eschweilera sagotiana</i>	1208
Parvifolia	<i>Eschweilera coriacea</i>	500
Parvifolia	<i>Eschweilera decolorans</i>	84
Parvifolia	<i>Eschweilera wachenheimii</i>	19
Parvifolia	<i>Eschweilera grandiflora</i>	14

Parvifolia	<i>Eschweilera pedicellata</i>	14
Symphonia	<i>Symphonia sp.1</i>	382
Symphonia	<i>Symphonia globulifera</i>	71
Talisia	<i>Talisia hexaphylla</i>	60
Talisia	<i>Talisia praealta</i>	37
Talisia	<i>Talisia simaboides</i>	31

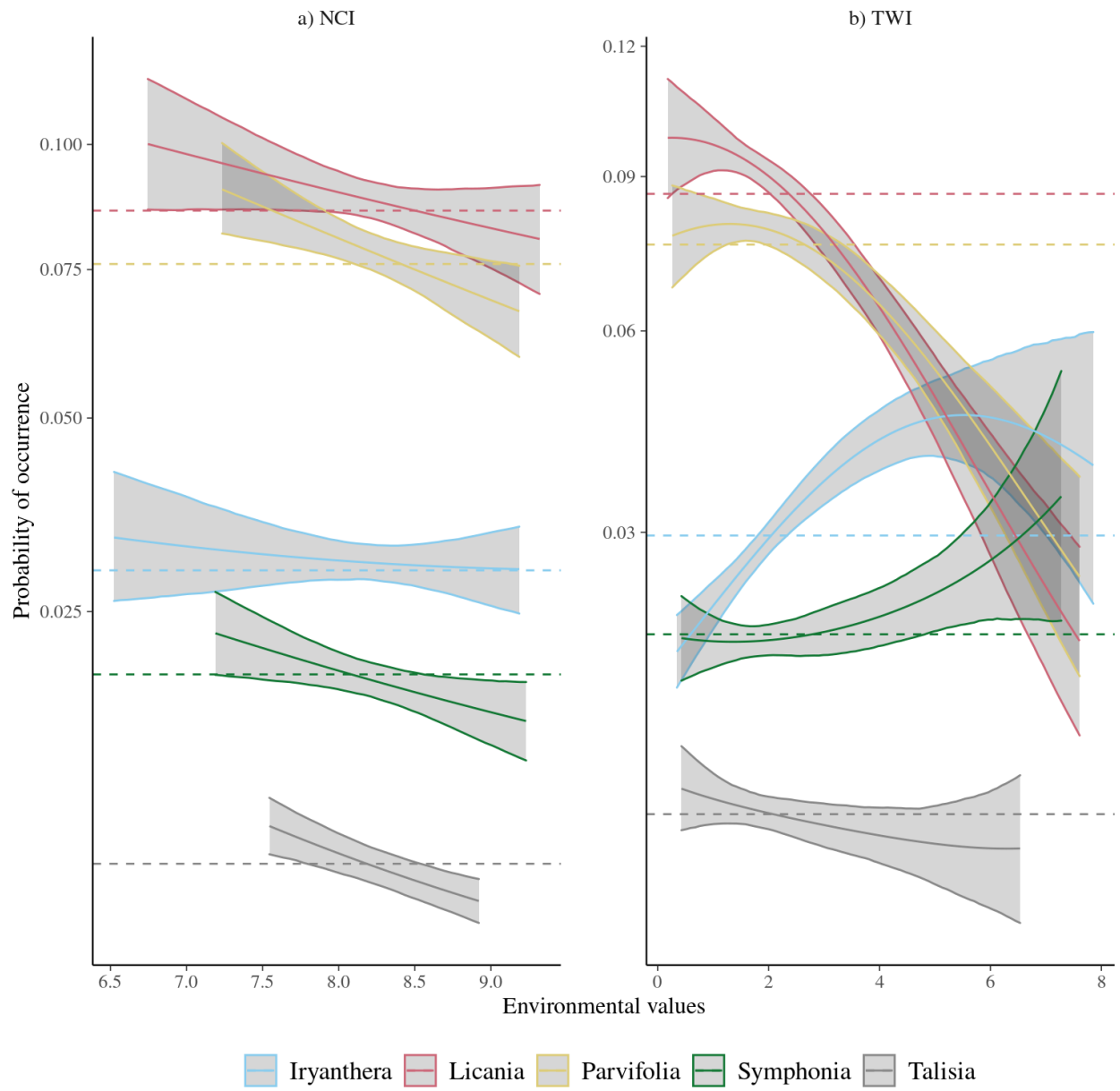
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## Figure legends

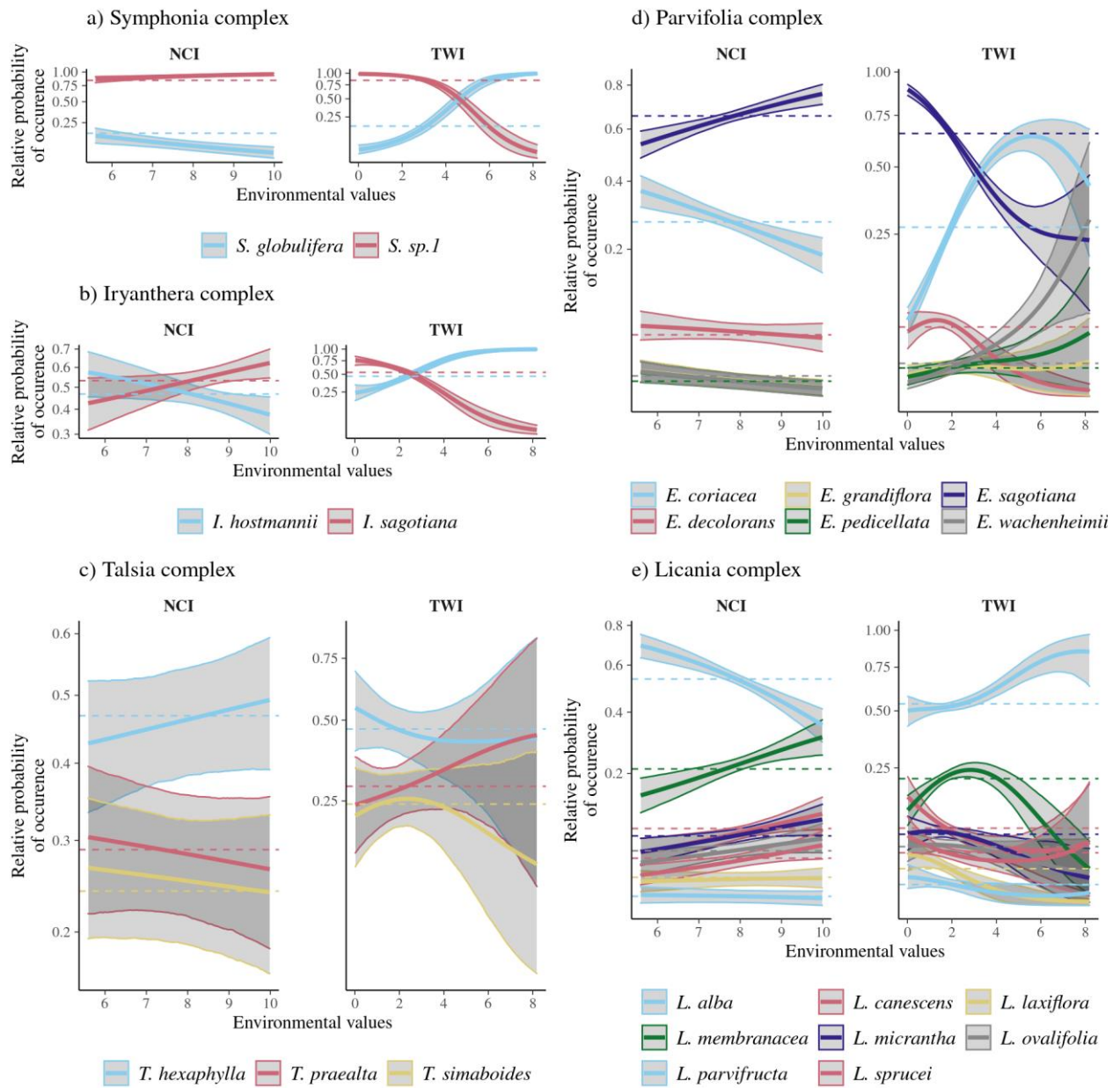
**Figure 1** *Predicted probability of occurrence for studied species complexes in Paracou. Lines and shaded areas represent mean and the 95% confidence interval of projected probability of occurrence of species complexes depending on a) NCI (left) and b) TWI (right), with the other variable set to its mean value. Dashed lines represent the observed mean relative abundance of each species complex in Paracou. Species complexes are indicated by different colors*

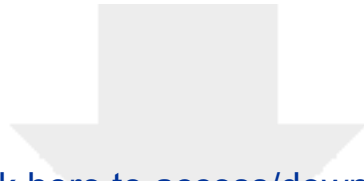
**Figure 2** *Predicted relative probability of occurrence for species within five species complexes in Paracou a) Symphonia; b) Iryanthera; c) Talisai; d) Parvifolia; e) Licania. For each complex, projected relative probability of occurrence of species is shown depending on NCI (left) and TWI (right), with the other variable set to its mean value. Dashed line indicates the observed mean relative abundance of each species in Paracou. Species are identified by different colors.*

**Figure 1**



**Figure 2**





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**Supplementary Material**

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