

# 4 *Clusia* as Nurse Plant

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## 4.1 Introduction

The nurse-plant syndrome (see Franco and Nobel 1989) takes place when plant species shelter seedlings, young and/or adult individuals of other species through their ontogeny. The nurse-plant might then enhance fitness, survival and/or growth of associated species (Callaway et al. 2002; Bruno et al. 2003). However, positive and negative interactions are unlikely to occur separately in nature (Holmgren et al. 1997; Brooker and Callaghan 1998; Dickie et al. 2005). This balance is affected by spatial and temporal shifts (Morris and Wood 1989; Tielbörger and Kadmon 1997; Callaway 1998) related to plant ontogenetic development and/or changes in resource availability (Callaway and Walker 1997). For instance, the overall importance of positive interactions on community structure, such as the nurse-plant syndrome, is claimed to be higher in resource-poor environments (Callaway et al. 2002; Lortie and Callaway 2006).

This syndrome often results in the formation of vegetation clumps or islands (Pugnaire et al. 1996; Kikvidze and Nakhutsrishvili 1998; Weltzin and McPherson 1999) and is well known for arid and alpine zones. However, there are still a few examples from tropical environments. One such example of a nurse plant is *Clusia hilariana* Schltld., a species from the Brazilian restingas. Despite some field observations suggesting that a nurse plant effect might occur in the case of other CAM *Clusia* species in the Brazilian restingas (e.g., *C. fluminensis* Pl. and Tr. and *C. spiritu-sanctensis* Mariz and Weinberg), *C. hilariana* has been more thoroughly studied in this respect. This chapter revises such studies, aiming to discuss the extent and consequences of such effect on restinga vegetation. We also discuss which features of *C. hilariana* are likely to be responsible for such positive effects, which may serve as indication for other possible nurse species of *Clusia*.

## 4.2 Restinga de Jurubatiba: Phytosociology

*Clusia hilariana* occurs, often with high abundance, along the coast of south-eastern Brazil, particularly in northern Rio de Janeiro state and southern Espírito Santo state. The studies reviewed here were conducted in the Restinga de Jurubatiba National Park (22°00'–22°23'S; 41°15'–41°45'N), more specifically at the so-called *Clusia* scrub, a vegetation physiognomy that covers some 40 % of the ca. 14,000 ha of this Park and consists of hemispheric vegetation islands of various sizes surrounded by white sand (Chap. 3 and Sect. 9.4.2.1 provide detailed accounts of the restinga vegetation as a whole and of the particular vegetation of this Park).

*Clusia hilariana* is the *dominant* plant of this vegetation (Araujo et al. 1998, 2004). In phytosociological terminology, this means that this species has the highest *importance value* (IV), i.e. the sum of relative frequency, relative density and relative basal area, among plant species within a given sampled area (Müller-Dombois and Ellenberg 1974). Pimentel (2002) did a thorough survey of 12 sample areas using the line intercept method and sampled all woody plants  $\geq 50$  cm tall, on three parallel beach ridges that varied in respect to their distances from the sea. She found that the vegetation has an oligarchic structure (i.e., when the IV of only a few species add up to a high percentage of the total IV, in this case, the top 6 out of a total 62 species accounted for 49 % of the total IV of the vegetation), which is a pattern commonly found also in tropical forest formations, especially in disturbed or early successional communities (Pascal and Péliissier 1996), and in other open vegetation types marginal to the Atlantic rain forest (Scarano 2002).

Additionally, Pimentel (2002) found a Shannon diversity index ( $H'$ ; Magurran 1988) of 3.07. This index is given by

$$H' = -\sum p_i \times \ln p_i$$

where  $p_i$  is the ratio of the number of individuals ( $n_i$ ) of a species  $i$  to the total number of individual plants ( $N$ ) on the selected area ( $p_i = n_i/N$ ).

This diversity value is lower than in typical Atlantic (e.g., Sanchez et al. 1999) or Amazon rain forests (e.g., Campbell et al. 1992), where it often ranges between 4.00 and 5.00. However, it is surprisingly high considering the extreme environmental conditions these plants are often subjected to (e.g., Scarano et al. 2005). This value was also higher than those obtained for other open woody restinga communities in southeastern Brazil, i.e. from 2.63 to 2.93 (Pereira et al. 2001), sampled by the same method. Pimentel (2002) argued that this high diversity resulted from the high number of species with low abundances and restricted distributions.

The fact that Liebig et al. (2001) found  $H'$  values of 2.70 underneath the canopy of male and female *C. hilariana* trees is an important indirect evidence

of the nursing role of this species. It has to be mentioned, however, that this study included all plants whereas Pimentel (2002) sampled only woody plants.

### 4.3 Evidences for Nurse Plant Effects

In order to irrefutably confirm the key role of *C. hilariana* as a nurse plant species, we would necessarily have to create experimental set ups in the field to simulate a situation where this species is not present, i.e. we would have to perform removal experiments. The removal and the eventual 'disappearance' of the species from a given point in space simulate a disturbance of such extent as to locally extinguish the species. Such experiments demand a huge logistic effort for set up, monitoring and analysis (Diaz et al. 2003 and Kareiva and Levin 2003 reviewed removal experiments). They also require special permits from environmental officials. However, before we designed such experiments, we decided first to gather additional observational data on plant-plant association and coexistence, on spatial variation regarding gender and ontogenetic stage of *C. hilariana* plants, and, more recently, to apply structural equation modelling (SEM) to assess which are the main causal factors related to the nursing effect. Thus, in the next two sections (Sects. 4.3.1 and 4.3.2) we review previous work, while in the last one (Sect. 4.3.3) we present original data analyses and discuss the applications of SEM as a non-destructive method to analyse patterns of species interactions.

#### 4.3.1 Association, Coexistence and Facilitation

The M.Sc. dissertation of Correia (1998) was the first study to propose a role for *C. hilariana* in facilitating germination and growth of other restinga plants. She examined population structure and interspecific pairwise associations between four woody species within a 0.5-ha plot in an open restinga site: *C. hilariana*, *Protium icicariba* (DC.) Marchand (Burseraceae), *Andira legalis* (Vell.) Toledo (Leg. Faboideae) and *Vernonia crotonoides* Sch.Bip. ex Baker (Asteraceae). While *Clusia* and *Protium* were the two most abundant species, *Vernonia* was intermediary in abundance and *Andira* was rare. She showed that adult *Clusia* had a positive association with their own juveniles and those of *Protium*, and that this pattern was clearer as the vegetation islands dominated by *Clusia* increased in size. This indirect evidence of facilitation was corroborated by a parallel dissertation conducted by Zaluar (1997) who demonstrated that underneath the canopy of *Clusia* there was higher species richness than under any other woody species.

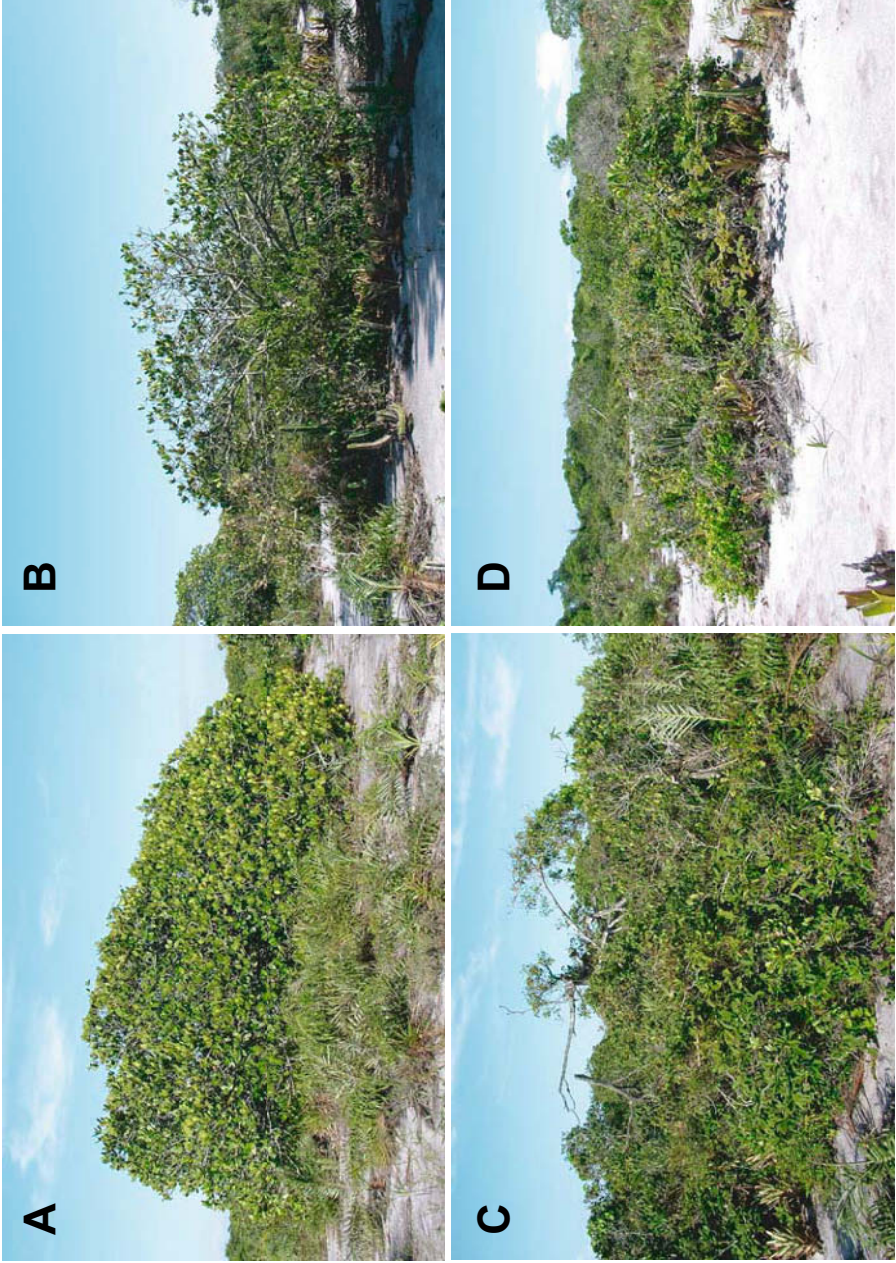
Another interesting finding of Correia (1998) was that a significant proportion of *Clusia* seedlings were found inside bromeliad tanks (see also Chap. 5

and Sect. 9.3). Thus, it would appear that the 'suspended soil' found within the tanks formed by bromeliad rosettes favours seed germination and seedling growth. This has also been found in the restinga of Barra de Maricá for *Clusia fluminensis* by Macêdo and Monteiro (1987) and Zaluar (2002). In short, our nurse plant is itself nursed by bromeliads. Scarano et al. (2004) presented a model describing the consequences of such plant-plant interactions to succession in the open restingas of the Restinga de Jurubatiba National Park.

Dias et al. (2005) produced the most conclusive evidence regarding the nursing effect of *Clusia*. This study compared the nurse role of patches with *Clusia* dominance vs patches without *Clusia* dominance (*Clusia* patches vs non-*Clusia* patches, henceforth), while examining differences in patch architecture (above-ground vegetation density and stratification) and woody species composition and size structure. Additionally, we performed an experiment of seed introduction for three woody species underneath these two types of patches and monitored germination, mortality and seedling growth over a one-year period. There was a positive association between the presence of adult *Clusia* and juvenile density of other woody species. This was attributed to architectural differences between the two patch types, where *Clusia* patches were more stratified, while non-*Clusia* patches were flatter and with a higher vegetation density (Fig. 4.1). These differences in patches could lead to distinct environmental conditions underneath the canopy and also distinct attractiveness to potential seed dispersers. However, in spite of the higher juvenile density in *Clusia* patches, there were no differences in germination rate and seedling mortality between the two patch types. This suggested that the understory of *Clusia* patches is not necessarily a better environment for germination and seedling survival than non-*Clusia* patches. The higher juvenile density and higher species richness of seedlings and juveniles on *Clusia* patches could result from a higher visitation of potential seed dispersers to this patch type. *Clusia* patches might provide preferential shelter and nesting sites for animals such as birds and bats in the restinga, because *Clusia*'s height and architecture makes it the most conspicuous plant in this vegetation type.

To investigate possible effects of *C. hilariana* on dispersal, we used the species similarity between the canopy (i.e., adult shrubs and trees that composed the canopy of the vegetation patches) and the understory (i.e., seedlings and juveniles of shrubs and trees) as an indirect assessment of between-patch seed dispersal, assuming that lower similarity between canopy and understory is a consequence of higher dispersal activity. The lower similarity between canopy and understory species in *Clusia* patches as compared to non-*Clusia* patches led us to conclude that there is a higher species invasion into the former patch type, which probably resulted from a greater activity of dispersers.

These results, however, required further examination on the mechanisms that drive plant interactions within patches, since some ambiguity was still



**Fig. 4.1A–D.** Different types of vegetation patches in the open vegetation of the Restinga de Jurubatiba National Park: **A** mature *Clusia*; **B** senescent *Clusia*; **C** dead *Clusia* with well developed understory; **D** plant patch without *Clusia* dominance

unsolved. For instance, the higher growth rates of introduced plants in non-*Clusia* patches seemed to contrast with the general observation that *Clusia* acts as a nurse plant. It thus appeared that despite possibly favouring seed arrival by improving the activity of dispersers, *Clusia* may later suppress plant growth in its understorey. Indeed, it has often been shown that preferred sites for germination are not always the best sites for plant growth (Morris and Wood 1989; Walker and Vitousek 1991) as competitive interactions may increase with time (Callaway and Walker 1997). A parallel can be traced to adaptive behaviour of individual species at different phenophases, where a change occurring during a critical period may be adaptive for a given phenophase while negative for later developmental stages (Amzallag 2005; see also Chap. 9, Sect. 5).

### 4.3.2 Gender and Ontogenetic Variation

As the evidences suggesting a nursing role of *Clusia* accumulated, we began to ask how repeatable this could be in space. This question seemed particularly relevant for two reasons.

First, our study species is dioecious, i.e. it has separate male and female individuals, while most Angiosperms are hermaphrodites (see Chap. 5). Several examples in the literature suggest that for dioecious plants, females tend to establish on sites with better growing conditions (Urbanska 1992; Crawley 1997), which can affect establishment of other species in the understorey. More obviously, female plants bear fruits that are also likely targets of potential dispersers of seeds of other species. Thus, Liebig et al. (2001) tested the hypothesis that female *Clusia* plants would nurse a higher diversity of species than males. The hypothesis was rejected, since the understorey of both male and female plants had Shannon diversity values ( $H'$ ) around 2.7 indistinctly. At that time, we interpreted that potential seed dispersers were not visiting *Clusia* plants in search for their fruits (that would mean a higher diversity associated to females), but in search for a resting place. In this case, there was no difference between genders, since their morphology was proven equal. In summary, the dioecious nature of *Clusia* did not imply spatial variation regarding its nurse role, i.e. the nurse plant effect occurs irrespective of gender.

Second, two other 'forms' of *Clusia* are distinguishable in the landscape: mature adults with a dense canopy vs senescent adults with canopy gaps (Fig. 4.1). Phenological studies showed that *Clusia* is an evergreen plant, with no marked timing for leaf production or leaf mortality (Rosado 2006). This suggests that senescent individuals are also older, or at least they are closer to the end of their life cycle. The M.Sc. dissertation of Ramos (2003) tested the hypothesis that senescent *Clusias* would nurse smaller species diversity than mature ones, due to plant death in the understorey caused by the changes in environmental conditions. She sampled all plants >20 cm in the

understorey of 12 mature *Clusia* plants and 12 senescent ones. Again, our hypothesis was rejected: there was no significant difference in plant species richness or diversity between patch types. This suggests that the nursing role of *Clusia* for most species probably takes place in the initial phases of seed germination and seedling establishment or, instead, that the effect of *Clusia*'s senescence might act only on a longer temporal scale not covered by our sampling.

However, the understorey of the senescent *Clusias* was on average taller and with a higher basal area than the understorey of the mature plants. These results conformed to the higher growth of seedlings on non-*Clusia* patches found by Dias et al. (2005) and fostered two alternative hypotheses: 1) When understorey plants reach a certain size and age, their growth is inhibited by *Clusia*, and is later resumed when *Clusia* senesces or dies. This had already been proposed by Dias et al. (2005) who suggested that the senescence and death of *Clusia* in a given patch could promote the growth of understorey juveniles and a change in architecture to a short and dense vegetation type. 2) When understorey plants reach a certain size and number they exert a strong competition over *Clusia*, which senesces and dies. Removal experiments would be essential to test which of the two hypotheses applies. Hypothesis 1 would require an experiment of *Clusia* removal, while Hypothesis 2 would require an experiment of understorey removal.

#### **4.3.3 Structural Equation Modelling (SEM): Mechanisms Behind the Nursing Effect**

Although the empirical data above helped to elucidate a number of processes related to the nurse plant effect of *Clusia* and to formulate new hypotheses, we still had a major gap as regards understanding of which mechanisms would be driving this effect. Thus, we needed an analytical method to allow hypothesis testing involving multiple interacting variables. The multivariate tool called "structural equation modelling" (SEM) seemed to be the appropriate alternative. We can trace the origins of SEM back to "path analysis", which was developed by Sewall Wright (1889–1988). However, its development until present is less than straightforward and results from various scholarly contributions (Bollen 1989). Although Wright was one of the most influential evolutionary biologists of the twentieth century, path analysis was largely ignored by his fellow colleagues. Further developments on this philosophical and methodological underpinning, leading to SEM, were mostly promoted under the scope of social sciences (Bollen 1989; Hoyle 1995; Pearl 2000; Shipley 2000).

To some extent, path analysis resembles multiple regressions in that it consists of a system of linear equations representing interactions between variables. However, unlike multiple regressions, path analysis deals with more

complex causal schemes that have more than one dependent variable and with interactions between these dependent variables. This method allows for the estimation of direct effects and indirect effects (i.e., the effect that is completely transmitted by some other variable, also called intervening variable) between variables, which can be pictorially represented by a path diagram, providing a synthetic scheme of the hypothesised relation between variables. The resulting partial correlations of path analysis are assumed to represent causal relations between variables, but they do not test causal links. Only with the development of new estimation techniques it was possible to test the whole causal model, with its implied statistical constraints, solving the main weakness of the path analysis as proposed by Wright. This allowed to test whether the statistical constraints implied by the hypothesised causal model agreed with observations, allowing falsification of the hypothesised causal structure (see Shipley 2000 for a brief SEM historical review).

The estimated coefficients of SEM represent the relation between two variables when all other variables of the model are kept constant at their means (i.e., partial covariance). At the same time, possible effects between variables not specified by the model are restricted to zero (i.e., covariance equals zero), thus providing a method for control of confoundings (Pearl 2000; Shipley 2000). The system of structural equations can be expressed on the matrix form as follows:

$$y = Bx + \Gamma x + \zeta$$

where  $y$  is the column vector of dependent variables;  $x$  is the column vector of independent variables,  $B$  is the matrix of the effect coefficients between dependent variables,  $\Gamma$  is the matrix of the effect coefficients of independent variables on dependent variables and  $\zeta$  is the column vector of errors in the equations (Bollen 1989).

Although the use of SEM is still restricted in ecology, one can already find publications in different sub-disciplines such as ecophysiology (Shipley et al. 2005), interaction ecology (Cariveau et al. 2004), community and ecosystem ecology (Grace and Pugesek 1997; Kubota et al. 2004; Taylor and Irwin 2004; Weiher et al. 2004). In this section we reanalysed data of Dias et al. (2005) using SEM, in order to identify possible mechanisms by which *C. hilariana* facilitates the establishment of other species in the restinga. We also discuss the potential of this analytical tool for further studies on plant-plant interactions and ecosystem ecology.

As already discussed above (Sect. 4.3.1), *Clusia* patches provide a more important site for plant establishment as compared to non-*Clusia* patches, and this nurse effect is possibly related to dispersal activity (Dias et al. 2005). Here we exchanged the approach of comparing *Clusia* vs non-*Clusia* patches by one of measuring relative abundance of *Clusia*, i.e. a continuous variable. This allowed us to use SEM and test the possible mechanisms by which *Clusia*



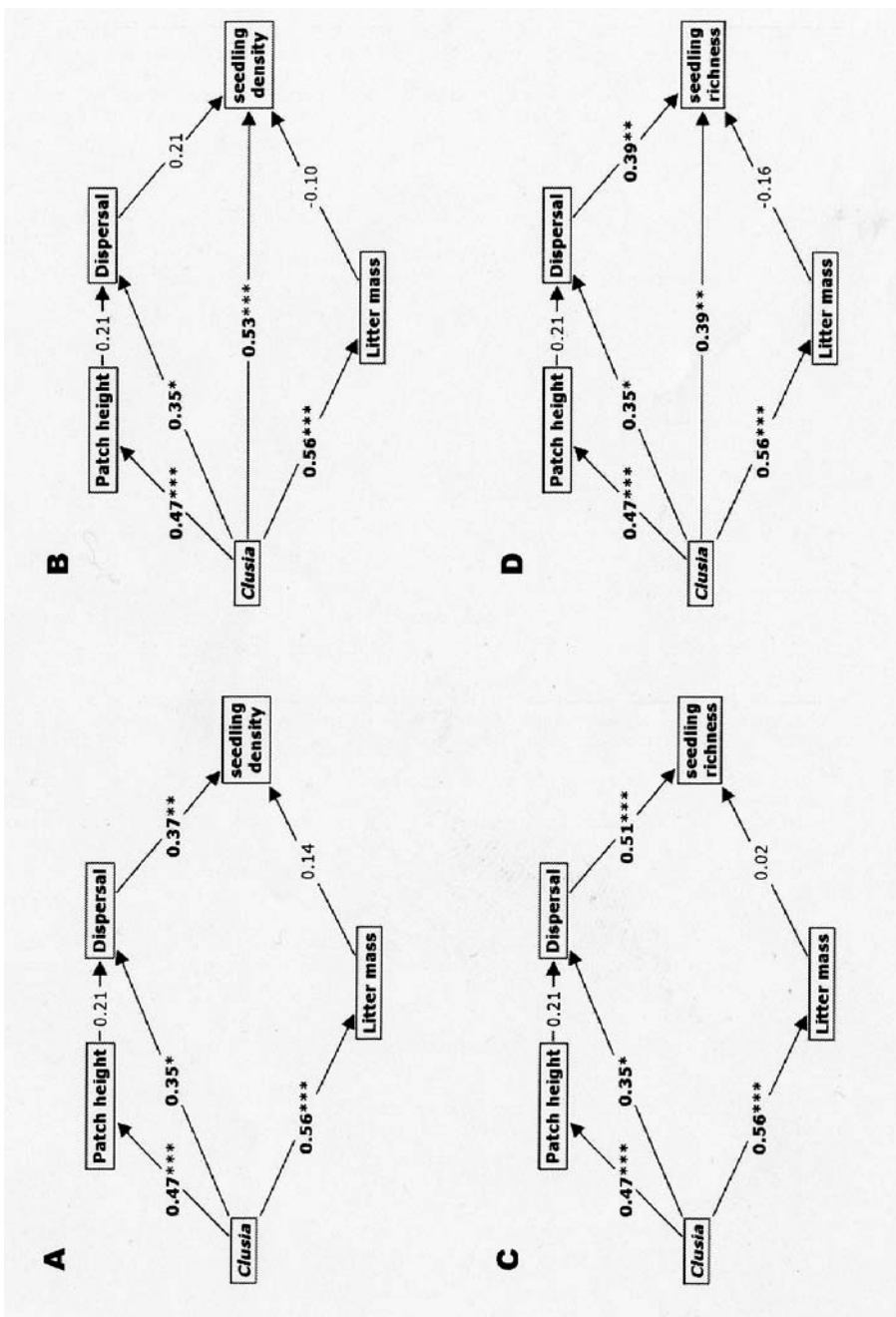
dominance affects seedling density and richness. The specified models test whether these effects are direct, or indirect through changes on dispersal activity. We also evaluated if the effect of *Clusia* on dispersal activity was due to patch height. *Clusia* patches are more conspicuous, which could promote higher visitation of potential dispersers (e.g., birds and bats). Our models also investigated the possible effect of *Clusia* on seedling density and richness through changes in litter accumulation. Since litter may physically impair seedling establishment (Berendse 1999) and *Clusia* promotes litter accumulation in plant patches (Dias et al. 2006), we expected an indirect negative effect of *Clusia* dominance on recruitment by increasing litter stock.

We tested the effect of *Clusia* separately for seedling density and seedling species richness. For both seedling density and richness we tested two alternative nested models; with (models B and D) and without (models A and C) a direct effect of *Clusia* (Fig. 4.2).

Maximum likelihood was used to estimate structural equation parameters with the R 2.0.1 statistical program (Bates et al. 2006) and SEM package (Fox 2004). We tested which of the nested competing models for seedling density (models A and B) and for seedling richness (models C and D) provided the most appropriated fit with data using chi-square test ( $\chi^2$ ), goodness-of-fit index (GFI), and adjusted goodness-of-fit index (AGFI). Models with a higher number of parameters to be estimated also have a higher probability to fit with data due to a lower number of degrees of freedom. The use of AGFI might correct this due to its penalties to model complexity (Hu and Bentler 1995).

As described by Dias et al. (2005), 30 vegetation patches, of at least 5 m diameter, were randomly chosen within the site. A 1x2 m plot was set in the middle of each vegetation patch. The central position of plots was chosen as to avoid edge effects. For assessment of recruitment process, all rooted plants within the plots were counted, identified and classified in two stage classes. Seedlings were plants <50 cm in height. For measurements of litter mass, one sub-plot (20 cm side) was randomly placed in each plot. All litter was collected within sub-plots and oven-dried at 50 °C until constant weight. A pin frame approach (adapted from Kent and Coker 1992) was used to determine *Clusia*'s relative abundance. A thin stick (0.8 cm diameter), sub-divided into four 90-cm sections, was positioned vertically in the plots to record: (1) the number of times the stick was touched by vegetation, (2) at which height interval each plant recorded touched the stick and (3) which species was touching the stick. This procedure was repeated every 0.5 m in each plot, adding up to 15 samples per plot. These 15 samples were pooled to comprise the total number of touches of the canopy, where only measurements above the first section (90 cm in height) were considered. The relative abundance of *Clusia* in the canopy was determined as the number of touches of this species divided by the total number of touches of the canopy.

We assumed that species similarity between canopy and understorey of a given vegetation patch negatively correlates to dispersal activity (Dias et al.



**Fig. 4.2A–D.** Path diagrams representing hypotheses about the effect of dominance of *Clusia hilariana* on seedling density and richness. For both seedling density and richness two alternative nested models were tested: A,C without a direct effect of *Clusia*; B,D with a direct effect of *Clusia*. Values in the arrows are the standardized parameters estimated by the models (\* $p < 0.06$ ; \*\* $p < 0.05$ ; \*\*\* $p < 0.01$ )

2005). Thus, we used the inverse of the Jaccard similarity index (Magurran 1988) as an index of dispersal ( $I_{\text{dispersal}}$ ). This index varies from zero (i.e., no species occur in both locations compared) to one (i.e., all species occur in both locations). For each vegetation patch we calculated:

$$I_{\text{dispersal}} = 1 - C_j$$

while  $C_j = j / (a + b - j)$

where  $C_j$  is the Jaccard index,  $j$  is the number of species common to both canopy and understorey,  $a$  is the number of species in the canopy and  $b$  is the number of species in the understorey.

The models for seedling density and richness, which predicted both direct and indirect effects of *Clusia*, provided a better fit with data. For seedling density, model A, which did not specify a direct effect of *Clusia*, did not fit the data. Its covariance matrix showed a marginally significant deviance from the observed covariance matrix ( $p=0.07$ ; Table 4.1), while model B, which specified direct and indirect effects of *Clusia*, showed good fit to data (Table 4.1). For seedling richness we observed a similar pattern. Although the covariance matrix of model C did not show a significant difference from the observed covariance matrix ( $p=0.15$ ; Table 4.1), model D, which predicted both direct and indirect effect of *Clusia*, showed a better fit to observations. Even AGFI, which penalises for model complexity, showed higher values for models that predict both direct and indirect effects of *Clusia* (Table 4.1). This suggests that there is an effect of *Clusia* via mechanisms that are not predicted by our models, which might play an important role in recruitment process.

The direct effect of *C. hilariana* on seedling richness was higher than the indirect effect due to the increase of dispersal (Table 4.2, Fig. 4.3). Perhaps more interesting is the fact that dispersal only affected seedling richness,

**Table 4.1.** Chi-square parameters ( $\chi^2$ ), goodness-of-fit-index (GFI) and adjusted goodness-of-fit-index (AGFI) for the models testing the effect of *Clusia hilariana* on the recruitment process. Models B and D include direct effect on seedling density and richness respectively, while models A and C do not include direct effects

	$\chi^2$	Degrees of freedom	Probability	GFI	AGFI
<i>Seedling density</i>					
Model A	8.65	4	0.07	0.90	0.62
Model B	1.68	3	0.64	0.97	0.89
<i>Seedling richness</i>					
Model C	6.72	4	0.15	0.92	0.69
Model D	2.59	3	0.46	0.97	0.83

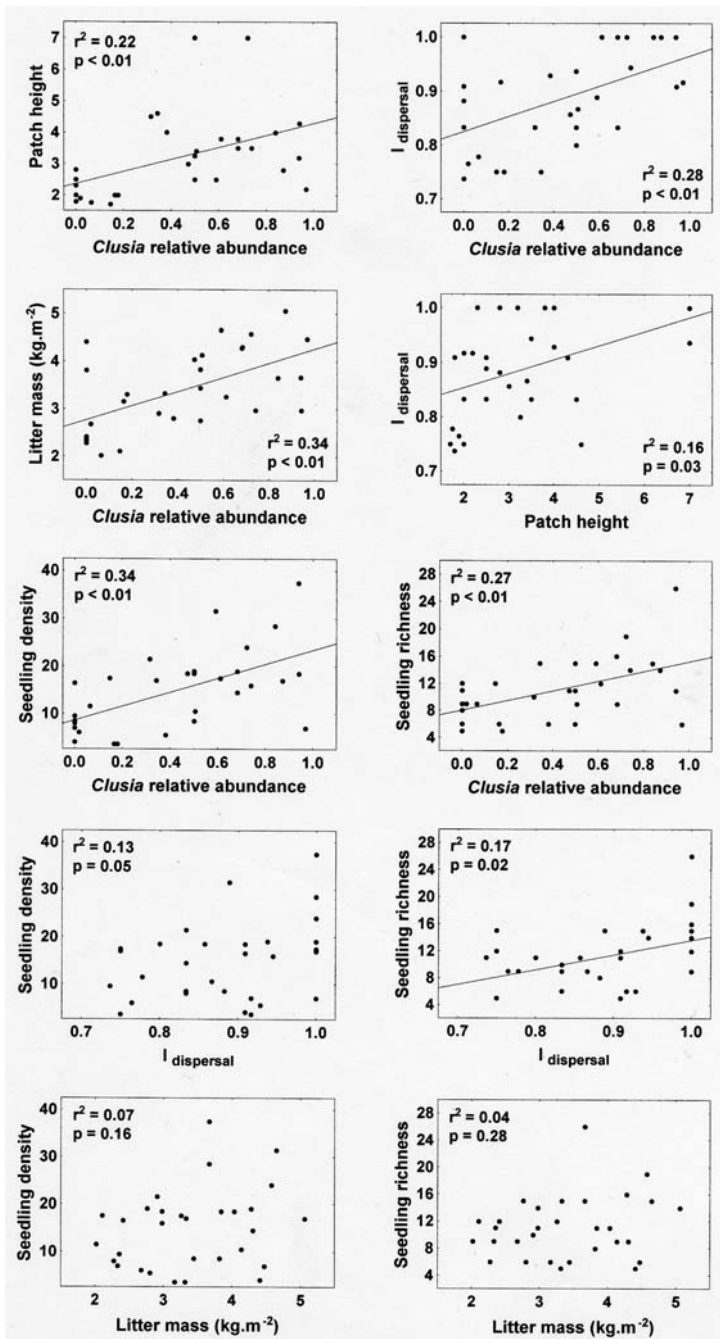


Figure 4.3. Bivariate plots of the variables (non-transformed data) used in the structural equation models. *Linear fittings* are shown for the relationships that were found significant

**Table 4.2.** Direct effect (DE), indirect effect (IE) and total effect (TE) of *Clusia hilariana* on seedling density and richness based on the accepted models

	DE	IE	TE
Seedling density	0.53	–	0.53
Seedling richness	0.39	0.14	0.53

since the effect of dispersal on seedling density disappeared when the direct effect of *Clusia* was included in the model. This shows that distinct processes regulate seedling density and seedling species richness. Between-patch dispersal might be important to increase within-patch seedling diversity but not to increase seedling density. Thus, we confirmed previous speculations (Liebig et al. 2001; Dias et al. 2005) and concluded that the effect of *C. hilariana* on community structure is, at least partly, due to its effect on seed dispersal.

In the model, dominance of *Clusia* also increased patch height, which is in harmony with our field observations that *C. hilariana* is the most conspicuous species locally. However, height alone is not responsible for enhancing activity of dispersers, indicating that there are probably other factors that might attract dispersers to *Clusia* patches. Although there was no effect of patch height on  $I_{\text{dispersal}}$  in our models, there was a significant relationship between these variables in the simple regression analysis (Fig. 4.3). This is a good example of how SEM can control for confoundings. The spurious relation between patch height and  $I_{\text{dispersal}}$  is probably due to the common cause shared by these two variables; i.e. *Clusia* dominance (Fig. 4.2). When *Clusia* dominance is statistically controlled, the relation between patch height and  $I_{\text{dispersal}}$  was no longer found.

Several works addressed the identity of dominant species as an important factor determining ecosystem properties, but there is still a lack of information of how these changes in ecosystem functioning can affect recruitment in natural communities (Suding et al. 2004; Weiher et al. 2004). We showed that dominance of *C. hilariana* positively affected litter stock; however, this ecosystem's property did not show any effect on seedling density or richness. The litter stock beneath *C. hilariana* in the restinga is high when compared to other open woody vegetation (Dias et al. 2006) but it does not act as an important physical barrier to seedling establishment. Considering that 70 % of the litter underneath *Clusia* canopy is composed by its own leaves (Silva 2003), it is to be expected that this species markedly affects nutrient cycling in the restinga. The effect of low litter quality of *Clusia* on decomposition can possibly influence nutrient availability to seedlings. The effect of *Clusia* on these and other ecosystems properties, and consequent effects on recruitment is the issue of future works. The use of SEM can help to disentangle such effects and provide a promising approach to study such indirect interactions.

## 4.4 Conclusions

*Clusia hilariana* is an important nurse plant in the restingas of northern Rio de Janeiro state. Previous field evidences were corroborated by the use of SEM and showed that this species has a positive effect on both understorey seedling density and richness. This process is partly related to the activity of seed dispersers that use male and female plants indistinctly. It remains unclear what happens later in the successional process: as understorey plants grow, they either get suppressed by *Clusia* or outcompete it. Removal experiments in the future shall prove useful to uncover further mechanisms and causal factors for such nursing effect.

In addition to the positive role played by *Clusia* on local biodiversity, recent evidence also indicates that *Clusia*, despite its conservative strategy of carbon acquisition via CAM, gives a high contribution to biomass stock in this nutrient-poor restinga (Dias et al. 2006). Thus, it might strongly affect ecosystems processes such as productivity and nutrient cycling that are also likely to affect recruitment process and, consequently, species composition. The use of SEM on future works will help to provide a synthetic framework of community and ecosystem dynamics.

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