UNIVERSIDADE FEDERAL DE SANTA CATARINA
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

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DEMOGRAFIA DE *CLUSIA CRIUVA* CAMBESS. (CLUSIACEAE) E A INFLUÊNCIA DAS INTERAÇÕES POSITIVAS PARA SEU ESTABELECIMENTO E SOBREVIVÊNCIA NO PARQUE MUNICIPAL DAS DUNAS DA LAGOA DA CONCEIÇÃO, FLORIANÓPOLIS, SC

Florianópolis

2010

Catalogação na fonte pela Biblioteca Universitária da
Universidade Federal de Santa Catarina

B413d Beduschi, Tatiane
Demografia de Clusia criuva Cambess. (Clusiaceae) e a influência das interações positivas para seu estabelecimento e sobrevivência no Parque Municipal das Dunas da Lagoa da Conceição, Florianópolis, SC [dissertação] / Tatiane Beduschi ; orientadora, Tânia Tarabini Castellani. - Florianópolis, SC, 2010.
100 p.: il., grafs., tabs.

Dissertação (mestrado) - Universidade Federal de Santa Catarina, Centro de Ciências Biológicas. Programa de Pós-Graduação em Ecologia.

Inclui referências

1. Ecologia. 2. Clonagem. 3. Gutifera - Reprodução. 4. Parque Municipal das Dunas da Lagoa da Conceição (Florianópolis, SC). I. Castellani, Tania Tarabini. II. Universidade Federal de Santa Catarina. Programa de Pós-Graduação em Ecologia. III. Título.

CDU 577.4

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Dissertação submetida ao Programa de Pós-Graduação em Ecologia da Universidade Federal de Santa Catarina para a obtenção do grau de Mestre em Ecologia

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Florianópolis

2010

Dedico esta dissertação aos meus pais, Ingrid Schmidt Beduschi e Hamilton Beduschi

Agradecimentos

Aos meus pais, pelo amor, dedicação e por toda a importância que sempre deram à minha educação, o que me permitiu chegar aqui. À ajuda prática de minha mãe, sempre disposta a ir a campo comigo, ou a tabelar os dados mais tediosos.

À minha irmã pelo seu companheirismo e conselhos.

À professora Tânia, melhor orientadora que alguém pode desejar. Possuidora de um conhecimento imenso, que sempre se esforçou em dividir comigo em todos estes anos de trabalho e amizade.

Às técnicas Karla Zanenga Scherer e Mara Lúcia Bedin, que, com toda a paciência, atendem a todos os inúmeros pedidos de ajuda.

Aos meus estagiários Diogo Costa Pereira de São Thiago, Laura Andrade Martins e Júlia Vieira da Cunha que tornaram possíveis e agradáveis as minhas incontáveis idas a campo.

Aos membros da banca Nivaldo Peroni e Flávio Antônio Maes dos Santos, por aceitarem colaborar com meu trabalho.

À CAPES pelo financiamento.

Ao Fernando Mayer por sua indispensável ajuda estatística.

À professora Ana Maria Vianna, pela identificação das gramíneas.

Aos professores da pós pelos ensinamentos nestes dois anos.

Aos colegas de laboratório e de corredor por todos os cafés compartilhados.

Aos amigos do mestrado pelas discussões, sugestões, festinhas e Ninas.

Aos amigos da época graduação por me darem a oportunidade de vivenciar uma amizade sem igual. Em especial agradeço à Giorgia Freitas Alves, Vanessa Moraes Nunes e Félix Baumgarten Rosumek, que me acompanharam no campo e nas festas (sempre até o final).

Aos amigos que não estudaram comigo, mas que me acompanham em eventos rock’n’roll.

Ao meu cachorro Snoopy, que faz minha vida mais feliz.

“Ilha do verde mirto e das flores vistosas,
Venerada afinal por todas as nações,
Onde suspiros de ardorosos corações
Flutuam como incenso entre jardins de rosas”
Charles Baudelaire

“A ciência é muito boa – dentro de seus preciosos limites. Quando transformada na única linguagem para se conhecer o mundo, entretanto, ela pode produzir dogmatismo, cegueira e, eventualmente, emburrecimento.”
Rubem Alves

Resumo

A restinga é um ambiente heterogêneo, no qual a vegetação pode formar mosaicos de vegetação herbácea e arbustiva. As condições abióticas severas encontradas neste ambiente podem impedir o estabelecimento de indivíduos. Por isso a propagação clonal, e as interações positivas (e.g. síndrome da planta-berçário), são importantes para possibilitar o recrutamento. *Clusia criuva* é uma espécie lenhosa e dióica, comumente encontrada em restingas e que pode se reproduzir clonalmente. Os objetivos deste estudo foram: analisar aspectos da demografia de *C. criuva* e a possibilidade da colonização na área ser recente; e investigar se existem interações positivas e, se elas têm um papel importante em processos populacionais da espécie. Todos os indivíduos em uma área de 38 ha foram marcados, medidos e georreferenciados. Um ano depois, a permanência de indivíduos nos quatro estágios de desenvolvimento (plântulas, juvenis, adultos vegetativos e adultos com flores) ou sua passagem para os estágios seguintes foi observada. O recrutamento (clonal e sexual) também foi observado e uma matriz de Lefkovitch foi construída. A distribuição espacial foi analisada usando a função K de Ripley. Para averiguar a existência de interações positivas, foram pesquisadas as espécies vegetais que ocorrem em associação com *C. criuva* e suas freqüências foram comparadas com as freqüências obtidas na amostragem sistemática. Além disso, foram feitos experimentos com germinação de sementes e sobrevivência de plântulas, em quatro tratamentos diferentes: áreas abertas, na borda de baixadas úmidas, dentro de bromélias e sob arbustos. Os resultados mostraram associação espacial positiva entre *C. criuva* e algumas espécies de arbustos, além de uma espécie de bromélia. Os experimentos revelaram que a germinação de sementes e a sobrevivência das plântulas nas áreas secas dependem da presença de outras espécies vegetais. Análises de fatores abióticos sugerem que a disponibilidade de água e a temperatura do substrato são as principais características amenizadas pelos facilitadores, que também podem estar agindo como poleiros, melhorando a dispersão de sementes. Indivíduos estabelecidos parecem ser capazes de sobreviver isoladamente e podem ter eliminado seus antigos benfeitores por competição. A distribuição agregada dos indivíduos, encontrada no estudo, também pode ser resultado das interações positivas e/ou advir da heterogeneidade ambiental. Um padrão de distribuição similar foi observado em indivíduos jovens e maduros. O crescimento em diâmetro e em altura foi mais expressivo em estágios pré-reprodutivos, mas adultos investiram mais em folhas. A permanência dos adultos nos respectivos estágios teve a maior contribuição para a taxa de crescimento populacional estimada (λ_{est}=1,02). Foi observada a reprodução clonal dos adultos vegetativos, mas todos os genetas recrutados são imigrantes. Quando comparados os valores das taxas de crescimento populacional calculadas (λ_{cal}) incluindo-se os imigrantes (λ_{cal}=1,53) ou os excluindo ((λ_{cal}=0,99) é possível perceber que o crescimento desta população depende de fontes externas de sementes. Todavia esta reprodução por sementes parece ser um fenômeno inconstante e a propagação clonal pode garantir a estabilidade desta população.

Palavras-chave: associação espacial, mecanismos facilitadores, colonização, reprodução clonal e sexual

Abstract

Brazilian coastal sand dunes are heterogeneous environments, in which the vegetation can form mosaics of herbaceous and shrub vegetation. The harsh abiotic conditions found in this environment can be prohibitive to the establishment of individuals. Therefore clonal propagation and positive interactions, (e.g. nurse plant syndrome), are important to enable recruitment. *Clusia criuva* is a woody dioecious species, common in coastal sand dunes that can reproduce clonally. The goals of this study were: to analyze aspects of the demography of *C. criuva* and to assess the possibility of a recent colonization of the area; and to investigate whether positive interactions exist and, if they have an important role in populational processes of this species. All individuals in an area of 38 ha were tagged, measured and their location was determined with a GPS. One year later, the stasis of individuals in the four developmental stages (seedlings, saplings, vegetative adults and flowering adults) or their passage to subsequent stages was recorded. Recruitment (both clonal and sexual) was also observed and a Lefkovitch matrix was constructed. Spatial distribution was analyzed using Ripley's K-function. In order to asses the existence of positive interactions, we investigated the plant species occurring in association to C. criuva and compared their frequency to a systematic sampling. Moreover, experiments on seed germination and seedling survival were performed, in four different treatments (open areas; in the border of humid slacks; inside a bromeliad and beneath shrubs). The results demonstrate that *C. criuva* is positively associated to some shrub species and one bromeliad. The experiments performed revealed that germination and seedling survival on dry areas depend on milder on the presence of other plant species. Analyses of the abiotic conditions in the experiments sites, suggested that water availability and temperature of the substrate are the main characteristics ameliorated by the benefactors that can also be working as bird perches, improving seed dispersal. Established individuals seem to be able to survive in isolation and may have outcompeted their benefactors. The clustered spatial distribution of the individuals, found by the study, can also be a result of the positive interactions and/or due to environmental heterogeneity. A similar distribution pattern was observed in young and mature individuals. Growth in height and stem diameter was more expressive in pre-reproductive stages, but adults invested more in leaves. Stasis of adults (which can reproduce clonally) had the greatest contribution to the population growth rate (λ=1.02). Clonal reproduction of vegetative adults was observed, but all recruited genets were immigrants. When the calculated growth rate of the population (λ_{cal}) with and without the immigrants (λ_{cal}=1.53 and 0,99, respectively) are compared, it is possible to notice that this population depends on external sources of seeds to grow. However, reproduction through seeds appears to be an inconstant phenomenon and clonal propagation may guarantee the stability of the population.

Keywords: spatial association, facilitative mechanisms, colonization, clonal and sexual reproduction

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1. Introdução

1.1 Restinga

As restingas estão inclusas no Domínio Mata Atlântica (Lei n.º 11.428/2006). Muitas de suas espécies vegetais são originárias da Floresta Ombrófila Densa, mas se adaptaram às condições extremas encontradas nos ambientes costeiros (Scarano, 2002). Restingas e dunas de areia cobrem cerca de cinco mil quilômetros (79%) do litoral brasileiro (Araújo e Lacerda, 1987). Na Ilha de Santa Catarina, a restinga representava, originalmente, 7% da cobertura vegetal, mas 22,4% deste total foi desmatado até 1978 (CECA, 1996). As restingas catarinenses têm origem quaternária e são formadas, principalmente, por dunas e suaves depressões (Falkenberg, 1999). Segundo Suguio e Tessler (1984), as planícies quaternárias brasileiras se formaram por ação conjunta dos seguintes fatores: fontes de areia (escarpas arenosas, rios, escarpas cristalinas e areias que recobrem a plataforma continental); correntes de deriva litorânea; variações do nível relativo do mar e deposição de sedimentos. Os agentes geológicos modificam a fisionomia destes locais, tendo destaque a ação do vento.

Muitos são os fatores limitantes para o estabelecimento de plântulas em dunas. Os mais importantes são a pobreza de nutrientes e a falta de água no substrato. Alguns nutrientes provenientes da água do mar são superabundantes no solo durante um período de tempo, mas são rapidamente lixiviados. A salinidade em forma de aerossol ou presente no solo só permite a sobrevivência de plantas capazes de suportar o excesso de cloreto de sódio. A baixa capacidade de retenção de água do solo arenoso e a alta taxa de evaporação acarretam estresse hídrico. Além de altamente permeável, o solo arenoso é instável, o que causa erosão ou deposição de sedimento por ação das ondas e do vento, muitas vezes removendo as plantas ou promovendo o soterramento por areia. O vento também tem grande influência sobre a vegetação da restinga, por causar constante dessecação, além de manter em constante agitação as partes aéreas das plantas. A intensa luminosidade é outro fator prejudicial, pois oxida a clorofila e aumenta a temperatura. Outros fatores que podem inibir o estabelecimento de plantas nestes locais são: a temperatura do solo, a competição, a herbivoria, doenças e infecções por fungos, além das atividades humanas. (Bresolin, 1979; Hesp, 1991; Maun, 1994).

A restinga não é um ambiente uniforme. A existência de diferentes condições ambientais definidas, em parte, pela distância do oceano, forma um gradiente na vegetação que pode também se apresentar em forma de mosaico (Falkenberg, 1999), como ocorre no Parque Municipal das Dunas da Lagoa da Conceição, na cidade de Florianópolis, Santa Catarina. Neste mosaico, dunas fixas, semifixas e móveis são entremeadas por depressões que podem ser ocupadas por corpos d'água, formados a partir do afloramento do lençol freático. Em anos muito chuvosos, estas áreas úmidas ou alagadas podem ter até 60 cm de profundidade (Araújo e Lacerda, 1987).

1.2 Reprodução sexual e reprodução clonal

Para resistir às adversidades impostas pelo ambiente, as plantas da restinga apresentam adaptações, como folhas suculentas, esclerófilas, pubescentes ou cobertas de cera, fotossíntese CAM ou C_4, resistência ao sal, germinação de sementes em épocas favoráveis (de maior umidade ou de temperaturas mais amenas, por exemplo), entre outras (Hesp, 1991). Uma adaptação muito freqüente neste ambiente é a propagação vegetativa, que possibilita às plantas superarem as dificuldades associadas ao estabelecimento de plântulas e germinação de sementes (Cordazzo e Seeliger, 1988; Cordazzo e Costa, 1989).

Em plantas, a reprodução assexuada pode se dar através de agamospermia (i.e. produção de sementes não fertilizadas) ou pela produção de rametas (Crawley, 1997). Rametas são unidades potencialmente independentes fisiologicamente de um *geneta* e podem ter todas as funções comuns aos indivíduos não-clonais (Pan e Price, 2002). *Genetas*, então, são compostos de tecidos provenientes de um zigoto (Eriksson e Bremer, 1993). Há um espectro de formas de propagação clonal que podem ser observadas. Em um extremo estão as espécies que se propagam espaçadamente, se infiltrando na vegetação e maximizando contatos interespecíficos. Em outro extremo estão as espécies com rametas muito próximos, excluindo outras plantas do território do clone. Estas estratégias são chamadas de “guerrilha” e “falange”, respectivamente (Lovett Doust, 1981). No entanto, ambas as estratégias apresentam limitada capacidade de dispersão, o que resulta na distribuição agregada de indivíduos em pequenas escalas (Harada e Iwasa, 1996).

Como ressaltado por Pan e Price (2002), estudos ecológicos com plantas clonais devem levar em consideração não só a propagação por sementes (*genetas*) como também a clonal (*rametas*), visto que ambas colaboram para o sucesso reprodutivo e, consequentemente, para a adaptação da espécie. Esta visão discorda da idéia clássica de que a adaptação deve ser medida somente em nível de geneta, visto que os rametas seriam partes do geneta e a reprodução vegetativa seria igual ao crescimento vegetativo da planta (Harper, 1977; Turkington, 2010).

No entanto, rametas podem colaborar para o aumento da adaptação do geneta. A probabilidade de sobrevivência do geneta aumenta com o crescimento no número de rametas (Pan e Price, 2002) da mesma forma que aumenta com o crescimento em tamanho do indivíduo (Harper, 1977). Além disso, em ambientes heterogêneos, os rametas podem se expandir para áreas com diferentes concentrações de recursos e responder plasticamente, se especializando na captação de um recurso, que pode ser distribuído para os outros rametas, aumentando a produção de biomassa (Stuefer et al., 1996; Fischer e van Kleunen, 2002).

Silvertown et al. (1993) constataram que há um balanço de curto prazo entre reprodução vegetativa e sexual. Ou seja, o investimento em propagação clonal implica em um menor investimento na produção de sementes e vice e versa. A reprodução sexual é vantajosa para a manutenção da diversidade genética da população e para a dispersão a longas distâncias (Silvertown, 2008). Por isso, a propagação por sementes poderia ser mais importante na colonização de novos locais e após perturbações. Com o tempo, a reprodução sexual seria menos abundante e a reprodução clonal predominaria (Eriksson e Bremer, 1993). Contudo, muitas espécies vegetais mantêm a reprodução sexual, mesmo após o período inicial de colonização (e.g. Berg, 2002; Weppler, 2006). Provavelmente, a manutenção da propagação por sementes e sua importância dependem de diversas características das espécies, como habitat, capacidade de dispersão das sementes (a longas ou curtas distâncias), forma de propagação (guerrilha ou falange) e de como ocorre a propagação dos *rametas* (abaixo ou acima do solo) (Eriksson, 1989).

Tendo em vista que a restinga é ambiente heterogêneo e muito restritivo ao estabelecimento de plântulas (Scarano, 2002), estudos voltados aos mecanismos de recrutamento de indivíduos e estudos detalhados de demografia têm grande importância para entender o funcionamento da restinga como um todo.

1.3 Facilitação

Facilitação ou interação positiva é a relação entre organismos que beneficia pelo menos um dos participantes e não prejudica nenhum deles (Bruno et al., 2003). A facilitação é um fenômeno amplamente distribuído que afeta a produtividade, diversidade, distribuição e reprodução das plantas (Callaway, 1995). O conceito de facilitação é baseado nas idéias de Clements, de que a sucessão é uma seqüência de desenvolvimento, no qual cada estágio prepara o caminho para o próximo (Ricklefs, 2003).

A facilitação pode agir diretamente, através da modificação dos recursos ambientais, como luz e temperatura, umidade, nutrientes e oxigenação do solo. Indiretamente, pode ocorrer modificação da densidade (e.g. compactação) do substrato, proteção contra herbívoros, atração de polinizadores, concentração de propágulos, interação entre raízes, micorrizas e alteração da microflora do solo (Callaway, 1995).

A facilitação e a competição agem simultaneamente (Holmgren et al., 1997). Espera-se que a facilitação seja mais importante em condições abióticas mais severas e que a competição predomine em condições mais amenas (Bertness e Callaway, 1994). Esta teoria, chamada de '*Stress-gradient hypothesis*' (SGH), tem sido objeto de muitos estudos (Mulder et al., 2001; Tewksbury e Lloyd, 2001; Callaway et al., 2002; Franks, 2003a ; Cavieres et al., 2006) e sua validade e generalidade foram discutidas em uma série de artigos (Maestre et al.; 2005; Lortie e Callaway, 2006; Maestre et. al.; 2006) que culminaram em um artigo de consenso entre os autores (Maestre et al.; 2009). Os refinamentos da SGH propostos pelo artigo sugerem que o balanço entre facilitação e competição depende não só das características dos fatores abióticos (recursos ou não recursos) como também da estratégia (*sensu* Grime, 1977) de cada uma das espécies envolvidas.

A chamada *nurse plant syndrome* ("síndrome das plantas-berçário") destaca-se entre as formas de interação positiva e tem sido freqüentemente relatada para ambientes xerofíticos. As plantas consideradas "berçários" contribuem para a melhoria das condições para germinação, estabelecimento e/ou crescimento de outras espécies vegetais (Zaluar e Scarano, 2000). Muitos estudos já identificaram espécies de plantas-berçário. Tewksbury e Lloyd (2001) estudaram uma espécie arbórea do deserto de Sonora (*Olneya tesota*) e constataram que a riqueza e a abundância de espécies vegetais aumentaram sob a influência desta espécie em ambientes xéricos. Moro et al. (1997) constataram o mesmo para *Retama sphaerocarpa* em um ambiente semi-árido no sudeste da Espanha.

Em áreas de dunas costeiras, este processo parece ser de grande importância para estruturar a comunidade, visto que somente algumas espécies têm a capacidade de colonizar a areia descoberta, onde a temperatura pode alcançar 70°C (Scarano, 2002). Neste ambiente, a sucessão se dá através de processos de nucleação, em que a espécie nucleadora cria um ambiente favorável para o estabelecimento de outras espécies, que irão, eventualmente, substituir as espécies iniciais (Yarranton e Morrisson, 1974). Um experimento realizado por Franks (2003b), em dunas costeiras na Flórida, mostrou que a quantidade de sementes e a emergência de plântulas é maior sob plantas adultas do que em áreas abertas, o que pode explicar também o padrão agregado observado na vegetação. Outro estudo, realizado em restingas (Martínez, 2003), mostrou a relevância da facilitação em áreas de dunas. Foi observado que a densidade de adultos e de juvenis de gramíneas não-pioneiras foi de duas a seis vezes maior sob o arbusto pioneiro *Chamaecrista chamaecristoides*. A temperatura da superfície arenosa, a velocidade do vento e o acréscimo de areia foram significativamente reduzidos pelo arbusto. Um resultado semelhante foi observado em um outro trabalho, realizado nas dunas arenosas costeiras de South Wellfleet (Shumway, 2000). O arbusto *Myrica pensylvanica* influenciou positivamente o crescimento, a reprodução e o recrutamento das herbáceas *Solidago sempervirens* e *Amnophila breviligulata*. Esta facilitação ocorreu através do sombreamento e da maior quantidade de matéria orgânica presente sob seus arbustos.

Plantas do gênero *Clusia*, como *Clusia hilariana*, são vistas como plantas-berçário (Scarano et al., 2004), pois se associam positivamente com juvenis de outras e de sua própria espécie, podendo também aumentar a complexidade da vegetação ao longo do tempo. Estudos de campo demonstraram que as plantas do gênero *Clusia* são encontradas com o metabolismo ácido das crassuláceas (CAM ou MAC) obrigatório, fotossíntese C_3 obrigatória e comportamento CAM/C_3 intermediário, sendo as únicas espécies arbóreas e dicotiledôneas que apresentam fotossíntese CAM (Scarano et al., 2005; Lüttge, 2007). Logo, se mostram bastante adaptadas ao ambiente ensolarado da restinga. Além disso, possuem reprodução assexuada bem sucedida e freqüente (Scarano et al., 2004).

Apesar de algumas espécies do gênero *Clusia* facilitarem o estabelecimento de outras plantas da restinga, alguns estudos mostram que as *Clusia* podem ser facilitadas por bromélias para seu estabelecimento inicial. Devido às condições desfavoráveis para germinação de sementes oferecidas pela restinga, as plantas da família Bromeliaceae podem ser um excelente berçário para outras espécies. Foi observada a presença de sementes e plântulas do gênero *Clusia* (*C. lanceolata* e *C. fluminensis*) no interior de bromélias, em trabalho realizado na Restinga da Barra de Maricá (RJ) (Macedo e Monteiro, 1987). Plântulas também foram encontradas em moitas onde não havia plantas adultas, o que indica que as sementes chegaram às bromélias através de algum agente dispersor.

Já foi evidenciado o efeito facilitador da exótica *Eucalyptus sp.* para o estabelecimento de *C. criuva* e de outras espécies de plantas arbustivas e arbóreas de restinga, no Parque Municipal das Dunas da Lagoa da Conceição (Simões-Jesus e Castellani, 2007). Beduschi e Castellani (2008) também sugeriram ocorrer uma facilitação por parte da bromélia *Vriesea friburgensis* Mez (Bromeliaceae) para o estabelecimento de *C. criuva* em áreas de vegetação herbácea/subarbustiva de dunas internas. Esta relação, no entanto, não foi encontrada em área de vegetação herbácea/subarbustiva em baixadas e depressões secas ou pouco alagadas.

1.4 Justificativa

Dada a grande diversidade de mecanismos ecológicos ocorrentes na restinga, a estabilidade dos ecossistemas depende estreitamente da preservação de seus componentes biológicos (Araújo e Lacerda, 1987). Por este motivo, o estudo das estratégias de estabelecimento de espécies em restinga e dos processos que atuam na estruturação e desenvolvimento das comunidades vegetais é essencial. Uma melhor compreensão da singularidade das interações entre os diferentes organismos e da contribuição de cada espécie para a dinâmica do ecossistema pode embasar ações de conservação e restauração das áreas de restinga.

A supressão da vegetação destes locais pode ocasionar a formação de dunas móveis, afetando todo o ambiente costeiro e a população litorânea. Ainda assim, este habitat é pouco focado pelas políticas nacionais de conservação, devido aos baixos índices de endemismo e biodiversidade.

2. Objetivos

2.1 Objetivo geral

Com o objetivo de compreender a dinâmica populacional de *Clusia criuva* e o funcionamento dos mecanismos facilitadores em ambientes de restinga, o presente trabalho pretende responder às seguintes perguntas:

- Qual é a escala de agregação espacial de *C. criuva* na área?
- *C. criuva* é favorecida, em seu estabelecimento, por espécies de bromélias ou por espécies arbustivas?
- Este favorecimento ocorre sob condições mais extremas de hábitat?
- Quais são os mecanismos facilitadores envolvidos?
- Qual a contribuição da reprodução clonal e da reprodução sexual na dinâmica desta população?
- Qual a tendência de crescimento populacional atual no ambiente de duna em questão?

2.2 Objetivos específicos

Para responder estas perguntas, o presente trabalho tem como objetivos específicos:

- Descrever a abundância, o padrão espacial e as espécies vegetais que ocorrem junto à *C. criuva*;
- Avaliar se esta distribuição está associada à ocorrência de bromélias ou a espécies arbustivas;
- Testar se a germinação ou a sobrevivência das plântulas é maior em associação a determinadas espécies vegetais ou sob condições ambientais específicas;
- Avaliar os fatores abióticos (temperatura da superfície do solo; velocidade do vento, luminosidade; quantidade de matéria orgânica do solo, umidade relativa do ar e do solo);
- Descrever a estrutura populacional de *C. criuva* em estádios de desenvolvimento e avaliar a sobrevivência, crescimento e recrutamento atual na população;
- Projetar tendências atuais de crescimento através de uma matriz populacional de Lefkovitch;

- Avaliar quais componentes da matriz têm maior importância para a manutenção da taxa de crescimento populacional;
- Determinar qual a proporção de novos indivíduos que provém de reprodução clonal e de reprodução sexual e qual a importância de cada tipo de reprodução para a taxa de crescimento populacional.

3. Área e espécie de estudo

3.1 Área de estudo

O Parque Municipal das Dunas da Lagoa da Conceição, que se localiza na Ilha de Santa Catarina e se estende do sul da Lagoa da Conceição até a praia do Campeche com extensão de 563 ha (Fig 1), foi criado pelo Decreto Municipal nº 231/1988 (CECCA, 1997). As dunas estão protegidas pelo Código Florestal Lei Federal nº 4771, de 15/09/1965) e pela Resolução nº 303/2002 do CONAMA,

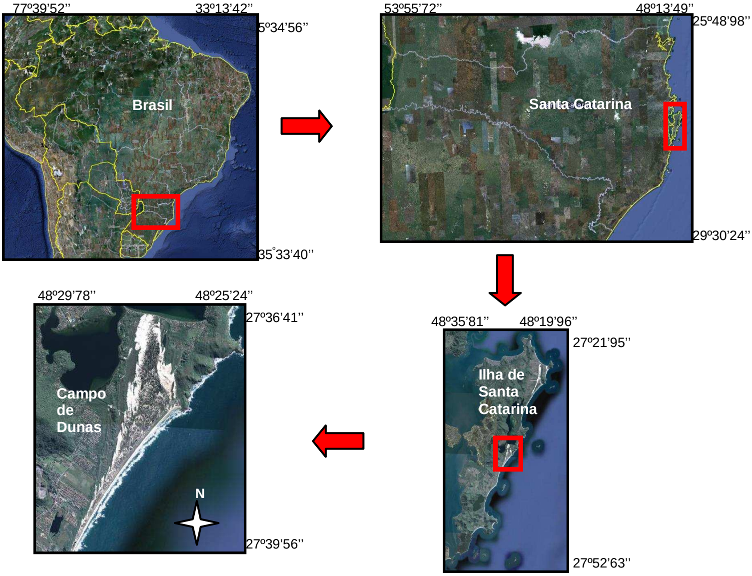

Figura 1. Localização do campo de dunas onde foi realizado o estudo. Parque Municipal das Dunas da Lagoa da Conceiçao, Ilha de Santa Catarina, SC (Fonte: Google Earth, 2010).

conseqüentemente, são consideradas Área de Preservação Permanente (CECCA, 1997). Estas dunas representam o principal complexo de dunas móveis e semifixas da Ilha de Santa Catarina (Bresolin, 1979).

Neste Parque, Güttler (2006) dispôs a vegetação em 12 classes (Tabela 1) de acordo com o porte da vegetação e dos hábitats de duna presentes no local: duna frontal, dunas internas, baixadas e depressões secas e alagáveis e corpos d'água.

Tabela 1. Tipos e subtipos de vegetação mapeados no Parque Municipal das Dunas da Lagoa da Conceição, Florianópolis, SC (Güttler, 2006).

Tipos de Vegetação	**Subtipos**
I. Herbácea/subarbustiva	a- Herbácea/subarbustiva da duna frontal
	b- Herbácea/subarbustiva de dunas internas
	c- Herbácea/subarbustiva de baixadas e depressões secas ou pouco alagadas
	d- Herbácea/subarbustiva de pequenos corpos d'água
II. Herbácea/subarbustiva/ arbustiva	a- Herbácea/subarbustiva/arbustiva de dunas internas
	b- Herbácea/subarbustiva/arbustiva de baixadas e depressões secas ou poucos alagadas
III. Arbustiva	a- Arbustiva sem espécie dominante
	b- Arbustiva da duna frontal dominada por *Dalbergia*
	c- Arbustiva da duna frontal dominada por *Eucalyptus*
IV. Arbustiva/arbórea	
V. Arbórea	
VI. Descaracterizada (ou ocupação urbana)	

O presente estudo foi realizado em uma região de dunas do Parque, selecionada, não pelo tamanho, mas sim pelo número de indivíduos e pela representatividade da amostra em relação à população. Esta representatividade foi admitida com base em observações prévias, que identificaram dois grupos bastante distintos em densidade de indivíduos e na morfologia dos mesmos (tamanho de folhas e número de ramos e folhas). Por este motivo, indivíduos dos dois grupos foram incluídos na amostra, de forma a retratar os diferentes aspectos da população e de seus indivíduos. Esta área mede 38 ha e contém os tipos de vegetação, segundo a classificação de Güttler (2006): herbácea/subarbustiva, herbácea/subarbustiva/arbustiva e arbustiva (Fig 2).

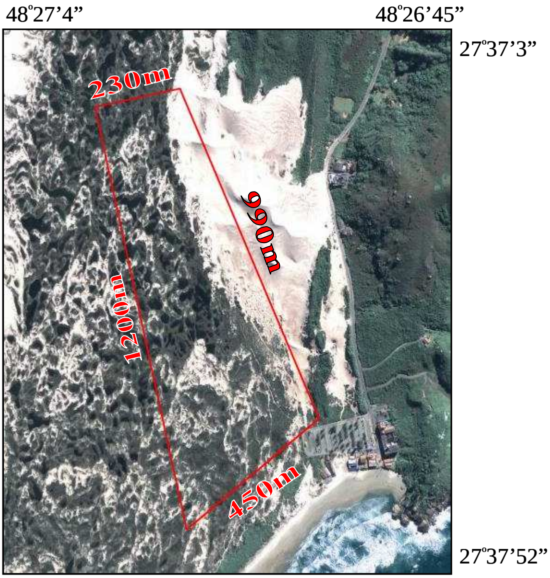

Figura 2. Foto de satélite do campo de dunas do Parque Municipal das Dunas da Lagoa da Conceiçao mostrando a área de estudo. Ilha de Santa Catarina, SC (Fonte: Google Earth, 2009).

A área não é homogênea. A porção sul, mais próxima do mar é mais seca, apresentando mais dunas e uma grande quantidade de bromélias *Vriesea friburgensis* (Fig 3). Gradualmente, nas áreas mais ao norte, as baixadas alagáveis e corpos d’água se tornam mais comuns e as dunas menos freqüentes (Fig 4). Nesta área, *V. friburgensis* se torna menos freqüente. Em toda a área de estudo são encontradas manchas com vegetação arbustivas, ora chamadas de ilhas de vegetação (Fig 5).

Figura 3. Porção sul da área de estudo, mostrando as dunas semifixas e as inflorescências de *Vriesea friburgensis*. Parque Municipal das Dunas da Lagoa da Conceição, Ilha de Santa Catarina, SC.

Figura 4. Porção norte da área de estudo, mostrando os corpos d'água e a predominância de vegetação herbácea.. Parque Municipal das Dunas da Lagoa da Conceição, Ilha de Santa Catarina, SC.

Figura 5. Ilha de vegetação encontrada na área. Parque Municipal das Dunas da Lagoa da Conceição, Ilha de Santa Catarina, SC.

3.2 Espécie de estudo

Clusia criuva Cambess. (Fig 6) pertence à família Clusiaceae e é conhecida popularmente como Mangue-bravo (Sampaio et al., 2005) ou Mangue-formiga (Falkenberg, 1999). É uma planta lenhosa, arbórea ou arbustiva, podendo também adotar o comportamento hemi-epifítico, tornando-se até estrangulante, o que deu origem ao nome de “mata-pau”, pelo qual as clúsias em geral são popularmente conhecidas (Joly, 1985; Zaluar e Scarano, 2000).

C. criuva é uma espécie dióica e que apresenta automimetismo, ou seja, as flores femininas (Fig 7a) mimetizam as masculinas (Fig 7b) para atrair os polinizadores, que são principalmente besouros. Apesar da agamospermia (produção de sementes não fertilizadas) já ter sido descrita para o gênero, *C. criuva* não apresenta este tipo de reprodução (Martins et al., 2007).

Os frutos de *C. criuva* (Figs 7c e 7d) são globulares, deiscentes e contêm cinco diásporos, com 0 a 17 sementes cada um. Os diásporos são envoltos por um arilo, que contém um dos maiores teores lipídicos (83,4%) já descritos na literatura. (Passos e Oliveira, 2002). Na Mata Atlântica, estas sementes ariladas são dispersas, primariamente por aves e secundariamente por formigas

É possível encontrar *C. criuva* em diversos ambientes, como na Mata Atlântica, na restinga, em florestas semidecíduas, em matas de galeria e em costões rochosos (Bresolin, 1979; Araújo e Scarano, 2007). Esta espécie só ocorre no Brasil e sua distribuição se estende da Bahia até o Rio Grande do Sul, ocorrendo também em Goiás e Minas Gerais, em altitudes menores de 1800 metros (Araújo e Scarano, 2007).

Figura 6. Aspecto geral de *Clusia criuva*. Parque Municipal das Dunas da Lagoa da Conceição, Ilha de Santa Catarina, SC.

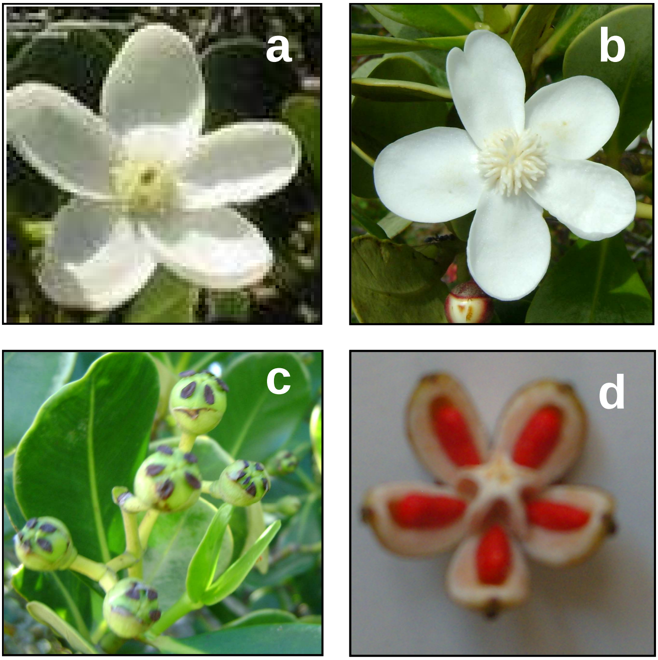

Figura 7. Estruturas reprodutivas de *Clusia criuva*. (a) Flor feminina (b) Flor masculina (c) Frutos verdes (d) Fruto maduro.

Na Ilha de Santa Catarina, a análise da composição florística das áreas de restinga realizada por Bresolin (1979) mostrou que *C. criuva* pode ser encontrada com grande expressividade em duas regiões: na restinga arbustiva do Pântano do Sul, sendo uma espécie bastante abundante, e na restinga do Rio Vermelho, onde, junto com *Ilex dumosa* e *Myrcia multiflora*, constitui cerca de 70% da cobertura superior da matinha litorânea. Em estudo mais recente, Guimarães (2006) detectou a presença da *C. criuva* em diferentes hábitats do Parque das Dunas da Lagoa da Conceição. Sua ocorrência foi considerada ocasional em baixadas eventualmente alagadas e rara em dunas fixas e semifixas. Em baixadas secas há ocorrência da espécie, mas sua abundância não foi estimada. Nesta mesma localidade, exemplares de *C. criuva* foram encontrados sob as moitas de *Eucalyptus* sp. por Simões-Jesus e Castellani (2007).

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Capítulo escrito em forma de artigo, seguindo as normas do periódico ***American Journal of Botany***

Capítulo 1

Demography, spatial distribution, individual growth and the relative importance of clonal and sexual reproduction of a woody species in a coastal dune environment

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Abstract

Brazilian coastal sand dunes are heterogeneous environments, in which the vegetation constitutes mosaics of herbaceous and shrub vegetation. Clonal propagation is a common adaptation found in these locations, and enables the recruitment of new individuals, since the harsh conditions limit germination and seedling survival. *Clusia criuva* is a woody dioecious species, common in coastal sand dunes that can reproduce vegetatively. In order to understand the population dynamics of this species and to determine whether its colonization in this habitat is recent. We have analyzed the spatial distribution, individual growth, demography and the importance of clonal and sexual reproduction to *C. criuva*. All individuals in an area of 38 ha were tagged and their location was determined with a GPS. One year later, the stasis of individuals in the four developmental stages (juveniles, saplings, vegetative adults and flowering adults) or their passage to subsequent stages was recorded. No regressions were observed. Recruitment (both clonal and sexual) was also observed and a Lefkovitch matrix was constructed. Spatial distribution was analyzed using Ripley's K-function. Results showed that this population is distributed in clusters of approximately 10 meters, probably due to environmental heterogeneity and positive interactions with other plant species. A similar distribution pattern was observed in young and mature individuals. Growth in height and stem diameter was more expressive in pre-reproductive stages, but adults invested more in leaves. Stasis of adults (which reproduce clonally and sexually) had the greatest contribution to the estimated population growth rate (λ=1.02). Recruitment of genets only happened by immigration of seeds, but contributed greatly to the growth of the population. However, reproduction through seed appears to be an inconstant phenomenon. This population appears to be colonizing the area and still depends on external input of seeds to grow, since the clonal propagation only compensates the mortality of individuals.

Keywords: *Clusia criuva*, population, Lefkovitch matrix, colonization, clonal and sexual reproduction

Introduction

Brazilian coastal sand dunes were formed by variations in the sea level from the Quaternary period and subsequent sediment deposition and are constantly transformed by the wind (Suguio and Tessler, 1984). The vegetation that covers this soil is a mosaic of plant communities, and "vegetation islands" of woody vegetation can be found within areas of herbaceous vegetation (Falkenberg, 1999; Scarano, 2002). When compared to mesic ecosystems, species diversity, productivity and structural complexity are lower in these communities, as a result of the harsh conditions to which plants are subjected (Kachi and Hirose, 1983; Scarano, 2002). Burial, strong winds, substrate erosion, flooding, salt sprays, drought, high salinity and lack of nutrients are some of these limitations (Hesp, 1991; Maun, 1994; Scarano, 2002). To endure in this environment, plants present adaptations such as small size, flexible stems, long and numerous roots, salt glands and leaves resistant to desiccation (Bresolin, 1979; Waechter, 1985; Hesp, 1991; Maun , 1994).

The initial colonization of coastal sand dunes is constrained mainly by sand burial and absence of organic matter (Olff et al., 1993; Lichter, 2000). Therefore, species that can endure such conditions are the first to establish. These species, which are usually herbaceous, but can also be shrubs, facilitate the establishment of later- successional species by gradually stabilizing the substrate and increasing the concentration of nitrogen in the soil (Connell & Slatyer 1977, Lichter, 1998, Martínez et al., 2001). However, this process is not homogeneous and spatial variation in stress factors like salinity, drought and flooding can lead to very different successional sequences in the same area (Olff, 1993). Similarly, evidences suggest that succession in coastal sand dunes can occur through nucleation. That means that the establishment of certain species brings changes in environmental conditions that enable other species to colonize the area beneath these individuals, forming patches the later coalesce (Yarranton e Morrison, 1974). Additionally, nucleation can happen when certain species accumulate the propagules of other species, which are able to germinate and establish, also generating a patchy distribution of individuals (Day and Wright, 1989; Franks, 2003; Martínez, 2003).

The spatial distribution of individuals is an important feature of a population. Since most of the interactions among individuals happen among neighbors (Harper, 1977), spatial distribution can be a key factor in population dynamics (Girdler and Radtke, 2006). Spatial patterns reflect processes that took place in the past and will determine processes occurring in the future (Law et al., 2009). A more regular pattern of distribution could be evidence of self-thinning, the density-dependent mortality that occurs progressively in cohorts as individuals grow in size (Begon and Mortimer, 1986; Wolf, 2005). Besides the nucleation processes mentioned above, clumped distributions can be formed by microsite mosaics, canopy gaps, vegetative reproduction or limited dispersal of the members of the population (Wolf, 2005; Law et al. 2009).

One strategy, common in this environment, is clonal reproduction (Cordazzo and Costa, 1989). In clonal plants, vegetative reproduction produces new ramets (i.e. clonal segments) by budding from roots, rhizomes, stems, storage organs such as tubers, leaves or inflorescences (Silvertown, 2008). This kind of reproduction allows plants to colonize limiting and heterogeneous environments (Stuefer et al., 1996). Given that the ramets can remain connected, photosynthates, water and nutrients can be transported between segments, increasing biomass incorporation (Mantuano and Martinelli, 2007). In heterogeneous environments, where resources are uneven distributed, clonal plants can respond plastically by a spatial division of labour or by growing to more favorable sites (Stuefer et al., 1996; Sampaio et al., 2004). The expansion of clonal plants can occur through shortly spaced ramets (phalanx strategy) or through widely dispersed ramets (guerrilla strategy) (Lovett Doust, 1981; Eriksson, 1989). Either way, clonal expansion limits long distance dispersal, as, over time, their expansion resembles that of an amoebae moving across the landscape (Robinson et al., 1992). Hence, it is hypothesized that sexual reproduction prevails in a clonal plant population during the initial colonization or after disturbance, but vegetative reproduction tends to dominate in established populations, when long distance dispersal is no longer needed. This model, however, is not valid for all plant populations (Eriksson and Bremer, 1993).

Plants of the genus *Clusia* are dioecious and can reproduce asexually. Some species can reproduce vegetatively or by agamospermy (seed production without fertilization) (Martins et. al., 2007), but this last kind of asexual reproduction has never been described to *Clusia criuva* Cambess. (Clusiaceae), which is the focus species in this study. As many of the species found in the Brazilian coastal vegetation, *C. criuva* originated in the montane Atlantic rainforest and migrated to the younger coastal lowlands (Scarano, 2002). The study of plant populations that originated in mesic conditions and adapted to a more extreme environment has a growing importance, considering the global warming scenario (Scarano, 2002). To our knowledge, this is one of the first studies describing the structure, distribution and dynamics of a species in such a situation. The exception is the research of Sampaio et al. (2005) that studied the ramet demography of the bromeliad *Aechmea nudicaulis* (L.) Griseb, a bromeliad also originated in the Atlantic rainforest.

To understand the dynamics of a *C. criuva* population in this coastal dune environment, we have addressed the following questions:

1. In what scale are the individuals of *C. criuva* clumped and what processes can be influencing the observed pattern?
2. How is the population structured and does this structure varies between years?
3. What components of the life-cycle contribute the most to the population growth rate?
4. What is the relative importance of clonal and sexual reproduction?

Material and Methods

Study area and plant species

The study was carried out within the coastal sand dunes of the Parque Municipal das Dunas da Lagoa da Conceiçao (27°37’S, 48°27’W). The climate of the region, according to Köppen classification, is humid subtropical, characterized by humid hot summers and mild winters (Caruso, 1990). Average monthly temperature is 21ºC, ranging from 16ºC in July to 25ºC in February. Mean annual precipitation is 1700 mm, with greater values in January and February and smaller values from June to August.

The dune system was originated during the sea level oscillations from the Quaternary period and the subsequent eolic sand deposition (Suguio and Tessler, 1984, Falkenberg, 1999). The study site is composed by a central dunefield where semifixed dunes, humid slacks and small temporary lakes form a mosaic of habitats and vegetations. The dunefield is composed mainly by herbaceous vegetation and some shrubs, which can form clusters, called “vegetation islands”. This central region is surrounded by two corridors of arboreous vegetation. Previous observations have detected two groups of *C. criuva* individuals that differed in density and size. Therefore, the sampled area was placed so that both these groups would be at least partially included, what resulted in an area of 38 ha located on the central dunefield.

Clusia criuva is woody dioecious species that can be found in semidecidous forests, gallery forests, coastal sand dunes and in the Atlantic forest. This species can be shrubby, arboreous or hemi-epifhytic stranglers. In the study site, all individuals were shrubs. However, arboreous individuals can be found in the corridors of arboreous vegetation mentioned above. The fruits are very attractive to animals and the seeds are primarily dispersed by birds (Passos and Oliveira, 2002). In the area, *C. criuva* flowers from December to March and mature fruits can be found from January to March.

Population sampling

The field investigation was performed during 2008-09. In the first year, all the individuals of *C. criuva* (n=309) found inside the delimitated area were tagged and mapped with a GPS (Garmim eTrex). The height, number of leaves, number of branches and stem diameter (at soil level) were surveyed in every individual, using a digital paquimeter (Digimess 150mm/6”). All measurements were made in July/August 2008 and repeated one year later. New recruitments were searched for in 2009 and classified into seedlings or ramets. Ramets were defined as all new individuals connected to the adult through the roots, but other characteristics could be used to differentiate them from the newly recruited seedlings. Size of the leaves, much bigger in ramets was one of those. Hardness and color of the stem was also a very clear characteristic. When vegetative reproduction was observed, the source individual was identified.

Demographic model

Individuals were classified in four stages of development. Their fate was recorded from one year to the other and a Lefkovitch (Stage structured) matrix was constructed. A general model of the matrix can be seen in Table 1. **Juveniles** were considered to have stem diameters smaller than 2.7mm. Such small individuals were considered to be less than 1 year old and, consequently, recently recruited. This limit was set based on the maximum stem diameter reached by seedlings recruited in summer 2009 by the time the second census was made. Ramets recruited in the last year which had stem diameters smaller than 2.7mm where also placed in this stage. **Saplings** were non-branched individuals, whose stem diameters where larger than 2.7mm. Reproduction was not observed in either of these classes. **Vegetative adults** were branched and could reproduce clonally. **Flowering adults** were observed flowering at least once during the duration of the research. Seeds were germinated in laboratory conditions and no dormancy was observed.

Table 1. Population matrix of *Clusia criuva*. F_{ij} indicates production of new individuals (by clonal propagation - F_{31} and F_{32} - and by seeds - F_{41} and F_{42}); G_{ij} designates the passage from one stage to the other and S_{ii} represents the permanence of individuals in the same stage.

		Stage at time *t*			
		Juveniles	Saplings	Adults	Flowering
Stage at time t + 1	Juveniles	0	0	F_{31}	F_{41}
	Saplings	G_{12}	S_{22}	F_{32}	F_{42}
	Adults	G_{13}	G_{23}	S_{33}	R_{43}
	Flowering	0	0	G_{34}	S_{44}

The estimated population growth rate (λ_{est}) and the elasticities (proportional sensitivities) were calculated by the program Ramas EcoLab 2.0 (Akçakaya and Root, 1999). Elasticities are the percentual variation of λ_{est} caused by a proportional change in one of the elements of the matrix (Gurevitch et al., 2009), i.e., they indicate the contribution of demographic traits to λ_{est} (Caswell, 1989). To compare the population growth rate with and without immigration, the λ_{cal} was calculated for both cases according to the following formula:

$$\lambda_{cal} = \frac{\text{number of individuals in the population at time t + 1}}{\text{number of individuals in the population at time t}}$$

A chi-square analysis was performed to compare the mortality between stages (Zar, 1984). Since there was only one flowering individual, this stage was not included in this analysis to avoid bias.

Individual growth

A Kruskal-Wallis rank sum test and Wilcoxon paired-sample test were used to assess differences between developmental stages regarding rates of growth in height, stem thickening and increase in the number of leaves. These rates where calculated by the formula:

$$\text{Proportion of increase} = \frac{\text{final value (2009) – initial value (2008)}}{\text{initial value (2008)}}$$

Also here, the flowering was left out of the analyses and the software R version 2.7.2 (R Development Core Team, 2008) was used.

Spatial distribution

Ripley's function K(d) was used to evaluate the spatial distribution of *C. criuva*. This function, also known as second-order analysis, counts the number of points within a certain distance *d* of each point, with *d* taking a range of values (Dale, 1999). If individuals are aggregated, the observed K(d)-value will be larger than the expected value found for complete spatial randomness (CSR), a uniform Poisson process. If individuals are uniformly distributed, the observed K(d)-value is smaller than the expected. In order to calculate the critical values for the CSR, at a significance level of 0.05, a Monte Carlo test was performed (100 simulations) as proposed by Baddeley (2008). Ripley's K function assumes that the point pattern is spatially homogeneous, i.e. presents constant intensity. Since the coastal dune environment does not exhibit such homogeneity, the modification suggested by Baddeley et al. (2000) for inhomogeneous point-processes was used (Kinhom(d)). To account for edge effect, a correction was applied. When the circle defined by the distance *d* is not completely inside the study area, a weighting factor, proportional to the amount of the circle situated within the area, is used (Ohser, 1983). In this analysis, individuals found in the first census were separated in young (juveniles+saplings) and mature (vegetative adults+flowering adults) in order to verify if the spatial distribution of individuals is different in initial and more advanced stages. Analyses were performed using the software R version 2.7.2 (R Development Core Team, 2008) and the package Spatstat (Baddeley and Turner, 2005).

Results

In the first census, 309 individuals were found against 474 one year later. Without immigration, the final number of individuals would be 306. The calculated λ_{cal} for the population was 1.53 when recruited seedlings were taken into account and 0.99, and when the increment by migration was not considered. The estimated population growth rate (λ_{est}), that does not account for migration, was 1.02. Initial and final abundances in each stage can be seen in Figure 1. During the study year, 194 individuals were recruited in the area (183 in the juvenile stage and 11 in the sapling stage).

The number of individuals in the first stage increased greatly in the second year (Figure 1). Recruitment by immigrant seeds (168- 92%) contributed the most to this increase. Since only one flowering individual was found in the reproductive season of 2008/2009 and it was a male, the source of all seedling recruitments was external. Seeds probably came from the arboreous corridors that surround the area, located at least 200 meters away and all seedlings were considered to be immigrants. Also, production of ramets by the flowering individual was not observed. Consequently the reproductive values of the flowering stage were zero. Vegetative adults produced 15 new ramets in the first stage (stem diameters smaller than 2.7mm) and 11 in the second stage. The abundance of saplings and vegetative adults did not change greatly.

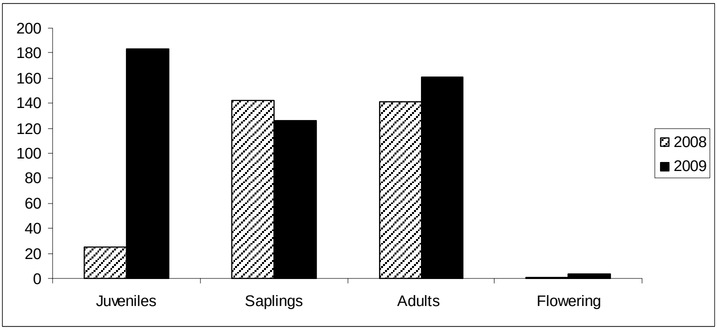

Figure 1. Number of individuals of *C. criuva* in each stage of development in two subsequent years.

According to the stages defined, retrogression was only possible between vegetative and flowering adults, but was not observed during the period of the study (Figure 2).

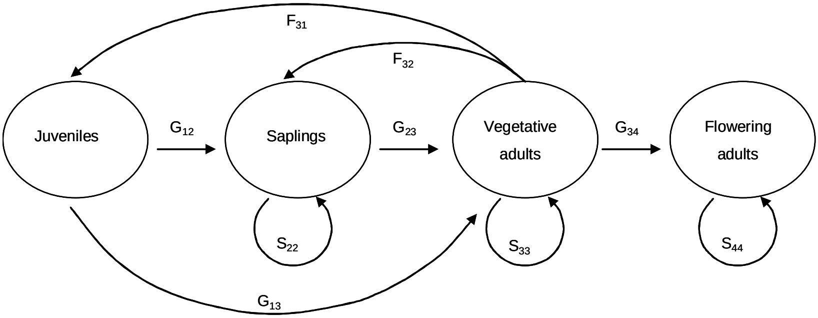

Figure 2. Life cycle graph of *Clusia criuva*. F_{ij} indicates production of new individuals; G_{ij} designates the passage from one stage to the other, S_{ii} represents the permanence of individuals in the same stage and R_{ji} represents the retrogression of individuals to previous stages.

The matrix contained the following components:

- F_{ij}= Fecundity (number of individuals produced by the stage *i* to the stage *j*/ number of individuals in stage *i* in time *t*.),
- G_{ij} = Growth (number of individuals that grew to stage *j*/ initial number of individuals in stage *i*),
- S_{ii} = Stasis (number of individuals that remained in the stage *i*/ initial number of individuals in stage *i*).
- R_{ji} = Retrogession (number of individuals that retrogressed to stage *i*/ initial number of individuals in stage *j*)

Considering that juveniles could not be older than one year old (i.e. were recruited in the last reproductive season), all individuals that survived passed to the next stage. In the other stages, however, there were high survival and stasis rates (Table 2). Three vegetative adults became flowering adults in the second year (two males and one female) and the one observed in the first year remained as flowering adult. By the time the second census was made, 29 individuals had died (3 seedlings, 16 saplings and 10 vegetative adults). Mortality was not different among stages (χ^2=1.556; p>0.05).

Table 2. Transition matrix of a population of *Clusia criuva* during a study performed in 2008/2009. Life cycle stages, population growth (λ_{est}) and abundance per stage (n=initial abundance/final abundance) are shown.

Λ_{est}= 1.02	Juveniles	Saplings	Adults	Flowering
n	25/183	142/126	141/161	1/4
Juveniles	0	0	0,11	0
Saplings	0,84	0,66	0,08	0
Adults	0,04	0,23	0,91	0
Flowering	0	0	0,02	1

Elasticity analysis revealed that changes in the proportion of vegetative adults remaining in the same stage had the highest effect on λ_{est} (Table 3). The stasis of saplings had the second greatest relative contribution to λ_{est}, followed by their passage to the subsequent stage. The stasis of the flowering individual, the production of juveniles by adults and the growth of juveniles into saplings contributed similarly. Vegetative adults becoming Flowering adults had the smallest effect on λ_{est}.

Table 3. Elasticity matrix of a population of *Clusia criuva* during a study performed in 2008/2009

	Juveniles	Saplings	Adults	Flowering
Juveniles	0,000	0,000	0,042	0,000
Saplings	0,039	0,135	0,035	0,000
Adults	0,030	0,074	0,626	0,000
Flowering	0,000	0,000	0,001	0,045

Regarding the spatial distribution, there was no considerable difference between the pattern observed for the mature and the young individuals (Figure 3 a e b).

In both cases, there was significant clustering at distances up to approximately 30 meters. However, cluster size is probably close to 10 meters, considering that after this level, the curve stabilizes, verging to random and uniform distribution, sequentially. This pattern is particularly clear with the young individuals. Repulsion of clusters was observed at distances greater than 40 meters. Two main clusters can be seen in the area, separated by 500 meters (Figure 4), as indicated by the UTM coordinates. Given that the spatial distribution was similar for both classes, all individuals were pooled in the graph. The greatest density is observed in the north of the area, farther from the sea.

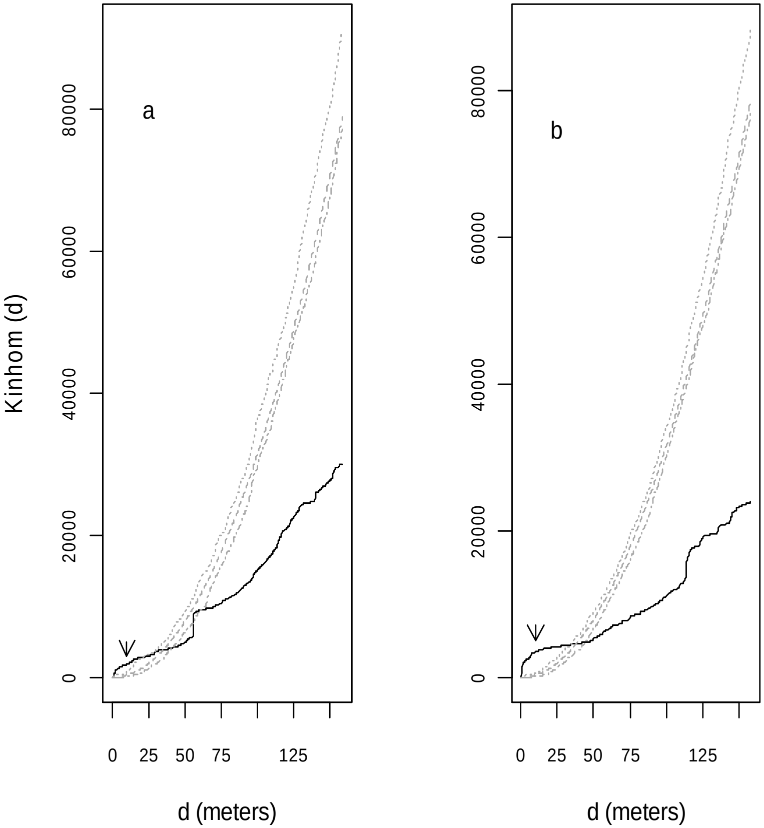

Figure 3. Spatial pattern analysis using Ripley’s K function. **(a)** Mature individuals **(b)** Young individuals. Solid lines represent the observed distribution and dotted lines represent values of Kinhom (d) and the 95% confidence interval for CSR. The arrows mark the 10 meters.

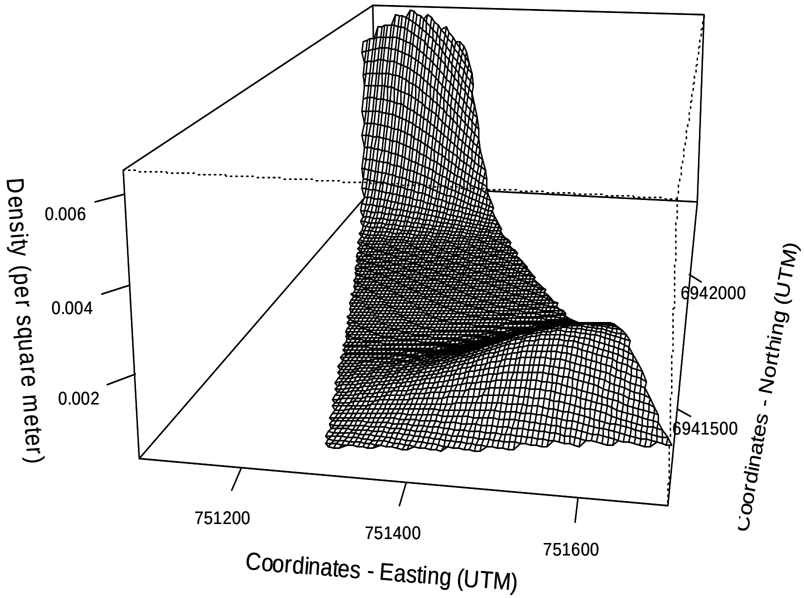

Figure 4. Density of *C. criuva* individuals in the study area. Coordinates (UTM) and density values are shown.

Individual growth was different between stages (Figure 5). Proportionally, juveniles invested more in diameter increase than the other two stages (Figure 5a). Vegetative adults grew less in height than juveniles and saplings (Figure 5b), but had the greatest proportional increase in number of leaves (Figure 5c). Some adult individuals had an enormous proportional increase in the number of leaves (3600%, 1671% and 1249%). To improve clarity, some of these outliers are not shown in the graphs.

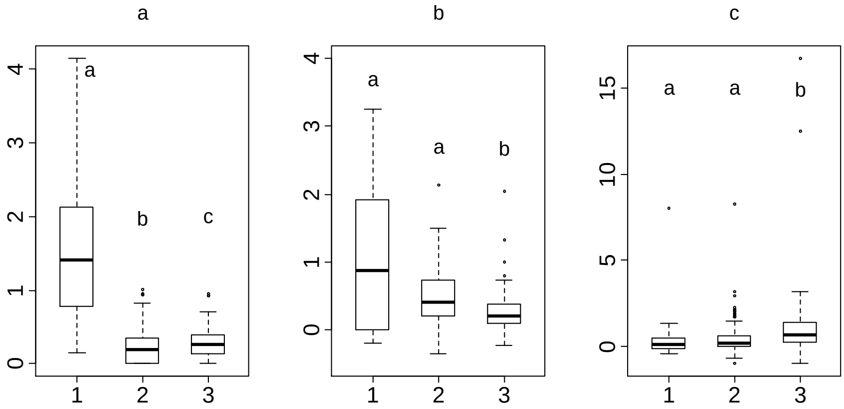

Figure 5. Growth of individuals in each stage. **(a)** Proportion of increase in stem diameter **(b)** Proportion of increase in height **(c)**Proportion of increase in number of leaves. 1- Juveniles; 2- Saplings; 3- Vegetative Adults. Central lines and boxes represent medians and first (1Q) and third quartiles (3Q), respectively. Whiskers represent 1.5 times the extent of the boxes (3Q-1Q) plus the value of the first and third quartile, for the lower and upper whisker, respectively. Points correspond to oultiers. To improve clarity, some outliers are not shown in the graphs.

Discussion

Based on field observations, the clusters observed at scales of approximately 10 meters appear to be consistent with the “vegetation islands” and with the scale of environmental heterogeneity observed in coastal sand dune vegetation. Clusters can arise from random variation in the initial colonization or by favorable local conditions (Levin, 1976). As few plants are able to colonize bare sand (which can reach very high temperatures) (Scarano, 2002), seedlings probably concentrate in the few favorable sites available. The presence and the density of some plant species can alter the dune environment and influence the distribution of other species as they provide milder conditions for the establishment of individuals (Shumway, 2000; Cheplick, 2005). Thus, these clusters are possibly formed by higher seed and seedling survival in limited areas, created by buffering plants, a process that can be particularly important in dry areas (Franco and Nobel, 1989; Leirana-Alcocer and Parra-Tabla, 1999). As observed in another study, seeds of

C. criuva do not germinate and seedlings cannot establish in the open dry areas of the dunefield, but are able to survive in association to other plant species (a shrub and a bromeliad) or in the border of humid slacks, where abiotic conditions are alleviated (Beduschi and Castellani, unpublished data). Clumped seedlings are expected to compete intensively and exhibit nonrandom mortality as they grow into larger classes (Girdler and Radtke, 2006). Nonetheless, no evidence of severe self-thinning has been found in this study, since the pattern of spatial distribution did not differ greatly between youngs and matures.

Due to the small number of flowering individuals, this population depends on the established individuals from the surrounding arboreous areas to recruit new genets, which contribute to the population growth (λ_{cal}= 1.53). Without this input, the population is merely stabilized (λ_{cal} = 0.99). As observed by Lichter (2000), the increase in seed availability can be an important factor favoring the establishment of populations of late-successional species during the colonization of coastal sand dune areas. Based on these facts, it is possible to suggest that this population is still colonizing this area.

Considering the great difference in number of juveniles between the years, recruitment was apparently much more expressive in the second year of the study, probably on account of the great amount of seedlings. In many clonal plant populations, seedling recruitment is an infrequent and irregular event and depends on “windows of opportunities”, such as favorable climatic conditions or disturbances (Eriksson and Bremer, 1993; Eriksson and Froborg, 1996; Holmgren and Scheffer, 2001; Weppler et al., 2006). In fact, a similar occurrence has been described for *Clusia hilariana* Schltdl., another species found in coastal dunes. Also for this species, abundant regeneration of seedlings could be a periodic phenomenon, but when it occurs, young plants originated by seeds are much more common than those originated by vegetative propagation (Martins et al., 2007). This pattern agrees with the results obtained in the present study, but contrasts with what was observed in other long-lived clonal plants, where vegetative propagation predominates (Clark-Tapia et al., 2005; Sampaio et al., 2005). This difference could be explained by the strategy of each population, since species with a phalanx growth form, which is the case of C. criuva, are expected to rely more on seed recruitment than guerrilla plants (Eriksson and Bremer, 1993). Also, the prevalence of ramets over genets tends to be more common in longer established populations than in younger populations (Silvertown, 2008). Clonal reproduction, although not very significant in the studied year, may guarantee population stability when sexual reproduction is not possible (Weppler et al., 2006; Silvertown, 2008).

Although clonal reproduction may compensate for mortality, even when there is no immigration, the stasis of vegetative adults had the greatest contribution to λ. Even though one year is a short period for conclusions about the dynamics of a long-lived plant, strong support is given in the literature to confirm that stasis of adults tends to be critical to the maintenance of population growth (de Kroon et al., 2000; Guedje et al., 2003; Forbis & Doak, 2004; Weppler et al., 2006), especially for woody long-lived plants (Silvertown et al., 1993). Accordingly, longer loops, such as those created by late reproduction, would contribute less.

Vegetative adults clearly invested less in growth (in height and in stem diameter) when compared to seedlings. Saplings exhibited an even smaller rate of stem thickening, but invested more in height. These results suggest that individual growth rate is not constant through the stages and a tendency to stabilization in higher stages can be observed. A study performed with another Clusiaceae, *Garcinia lucida*, also observed higher rates of growth (in this case, increment in diameter) in pre-reproductive stages (Guedje et al., 2003). Vegetative adults of *C. criuva* would, then, invest more in leaves or in the production of ramets. Those individuals with the greater values of increase in the number of leaves were almost leafless in the first census, probably due to herbivory. Therefore, any leaf found in the second census represented a great proportional increase.

Conclusions

This population of *C. criuva* is distributed in clusters, possibly because of the existence of few favorable sites of germination provided by other plants. There is a large proportion of the area still not colonized by this species. There is a dependence of the population on an external source of seeds, since only vegetative reproduction occurred. These observations indicate that the colonization of *C. criuva* in the area is recent. Large seedling recruitments appear to be irregular episodes and may depend on specific conditions. Therefore, clonal propagation and mainly stasis of vegetative adults, maintain the stability of the population.

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Capítulo escrito em forma de artigo, seguindo as normas do periódico ***Perspectives in Plant Ecology, Evolution and Systematics***

Capítulo 2

The influence of facilitation on germination, establishment and survival of a woody species in a coastal dune environment

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Abstract

Facilitation can have an important role in structuring natural communities. Possibly, the importance of facilitation increases with environmental severity and “nurse-plants” enable other species to establish and survive. In this study, the existence of positive interactions favoring germination and survival of the woody species, *Clusia criuva*, in a coastal dune environmental was examined. In an area of 38ha, we investigated the plant species occurring in association to C. criuva and compared their frequency to a systematic sampling, in order to verify the existence of positive spatial association. Moreover, experiments on seed germination and seedling survival were performed, in four different treatments (open areas, eventually covered by herbaceous vegetation; in the border of humid slacks; inside a bromeliad and beneath shrubs). The results demonstrated that *C. criuva* is positively associated to some shrub species and one bromeliad. The experiments performed revealed that seeds of *C. criuva* do not germinate and seedlings are not able to survive in open areas. Even though negative effects of the nurse plants on the seedlings, caused probably by shading, could be identified, establishment was improved and survival was enhanced in association to other plant species or in milder conditions. Analyses of the abiotic conditions in the experiments sites, suggested that water availability and temperature of the substrate are the main characteristics ameliorated by the benefactors that can also be working as bird perches and improving seed dispersal. Established individuals, however, seem to be able to survive in isolation, which may indicate that they have outcompeted their benefactors.

Key words: *Clusia criuva*, bromeliad, facilitative mechanisms, spatial association

Introduction

The concept of facilitation includes all processes by which a community, a population or an individual affects positively the performance of another individual, what includes enhancing its establishment, productivity or reproduction (Berkowitz, 1995; Callaway, 1995).

Facilitative mechanisms can take place directly, through the modification of environmental resources or conditions, such as light, temperature, water and nutrients availability and soil oxygenation, or indirectly, through the protection against herbivores, removal of competitors, concentration of propagules, root grafts, mycorrhizae and soil microbes (Callaway, 1995; Bruno et al., 2003; Rodriguez, 2006).

Several studies have indicated, not without controversy, that the importance of positive interactions increases in situations of higher "environmental severity" (*sensu* Brooker et. al., 2008), what is called the stress-gradient hypothesis (SGH) (Bertness and Callaway, 1994; Mulder et al., 2001; Tewksbury and Lloyd, 2001; Callaway et al. 2002; Cavieres et al., 2006, but see Maestre et al. 2005; 2006; 2009; Lortie and Callaway, 2006 for a more elaborate discussion). In coastal dune environments, plants are subjected to extreme conditions, namely drought, nutrient-poor unstable soils, strong winds, high soil temperatures and salinity (Bresolin, 1979; Hesp, 1991; Maun, 1994). In such an environment, many plant species depend on others to work as "nurse-plants" and improve the conditions of germination, establishment and/or growth (Tewksbury and Lloyd, 2001).

Spatial association among species is frequently used as an evidence of nurse effects and can result in patchy plant communities (Callaway, 1995; Fajardo et al., 2008). These patches are formed when pioneer species accumulate seeds and/or shelter seedlings and adults of other species under its canopies, in a process called nucleation, which is very important for succession in coastal dunes (Yarranton and Morrison, 1974; Day and Wright, 1989; Franco and Nobel, 1989; Franks, 2003).

Bromeliads are known to trap seeds of many species and, in some cases, to make germination possible (Macedo and Monteiro, 1987; Scarano, 2002). However, when facilitated plants do not have adventitious roots, which allows them to extend out of the bromeliads, seed accumulation can actually constitute competition, since the seedlings will not be able to establish and will die inside the bromeliad (Brancalion et al., 2009). Shrubs have also been identified as facilitators in coastal dunes. Simoes-Jesus and Castellani (2007) found that under the patches of the exotic shrub *Eucalyptus* sp. there was a greater establishment of woody species when compared to open areas. Plants of the genus *Clusia*, common in coastal dunes, have been described both as nurse-plants and as facilitated plants (Dias and Scarano, 2007; Simoes-Jesus and Castellani, 2007). Evidences of the bromeliad *Vriesea friburgensis* Mez (Bromeliaceae) acting as a benefactor to *Clusia criuva* Cambess. (Clusiaceae) were found by Beduschi and Castellani (2008).

In order to understand how woody species colonize coastal dunes, and based on previous evidences that indicate the influence of facilitation on this population of *C. criuva* (Beduschi and Castellani, 2008), the objective of this study was to corroborate the hypotheses that facilitation influences the distribution of this woody species and identify the mechanisms by which benefactors may act improving its germination, establishment, growth and survival. Since the effect of positive interactions can also depend on the size or quality of benefactors (Butterfield, 2009), two species (a shrub and a bromeliad) with different size, shape and life-form were examined.

The following questions were adressed: (1) Is there spatial association between individuals of *C. criuva* and another plant species? (2) Is recruitment more common in association to some plant species? (3) Is germination improved and survival of seedlings increased under any of the supposed benefactors studied or under milder environmental conditions? (4) What are the mechanisms of facilitation? (5) Are established individuals dependent on facilitation?

Methods

Study site and species

The study took place at the Parque Municipal das Dunas da Lagoa da Conceição located in the state of Santa Catarina, Brazil (27^o37’S, 48^o27’W). The dune field is constituted by shrubby patches on a matrix of herbaceous vegetation and surrounded by two corridors of arboreous vegetation. Eight kinds of habitat can be identified in the area: beach, frontal dune, internal moving dunes, internal semifixed dunes, internal fixed dunes, dry slacks, humid slacks, and flooded slacks (Guimaraes, 2006).

The study focused on the role of *Clusia criuva* Cambess. (Clusiaceae) as a beneficiary of facilitation. This is a woody dioecious species that can also present clonal reproduction. This species is widely distributed in the Brazilian coast and also in some non-coastal states. Its habitats include the Atlantic rainforest, semideciduous forests, gallery forests and coastal environments (Araujo and Scarano, 2007). In the study site, it can be observed on internal fixed dunes, internal semifixed dunes, dry slacks and on the border of humid slacks (Guimaraes, 2006).

The sampled area measured 38 ha and included slacks, dunes, herbaceous and sub-shrubby vegetation and vegetation islands (i.e. patches of shrubs). The corridors of arboreous vegetation were not comprised in the sampled area. All the individuals of *C. criuva* (n=301) were counted and tagged and their location was determined with a GPS (Global Positioning System) device so that recruitment and mortality of individuals could be identified. Only one reproductive individual was encountered, but, since it was a male one, all the seeds came from the adult trees on the adjacent arboreous corridors. It was also observed, for each individual, the kind of environment where it was located: patches of shrubs, open areas (eventually covered with sparse herbaceous vegetation), humid slacks or inside a bromeliad. Humid slacks were defined as low-lying areas, in which the soil was never dry and eventual or permanent flood could be observed (Grootjans et al., 1998).

Spatial association

By the time this part of the study was performed, 12 individuals were not found, probably because they were already dead. Recruitments were considered separately. Therefore, a total of 289 specimens of *C. criuva* were surveyed. All woody species occurring within a 0.5m radius of a *C. criuva* individual were surveyed and measured as well as all the herbaceous species whose coverage reached a minimum of 25 percent of the established area. Following the same procedure described above, a systematic sampling of the same size (n=289) was made in order to characterize the vegetation on the study area and compare the frequency (i.e. number of samples were the species was found / total number of samples) of the woody and herbaceous species with those detected in association with *C. criuva*. Six transects were laid out in the area, perpendicularly to the sea, and samples were taken each 20 meters, summing 50 samples per transect. Eleven samples were randomly chosen to be excluded from the sampling so that only 289 samples remained. A PCA was performed to investigate whether the vegetation found associated with *C. criuva* differed from the one recorded in the systematic sampling and what species contributed the most to this differentiation. This analysis was made using the software MVSP v 3.1 (Kovach, 1999). Afterwards, a chi-square analysis or a Fisher's exact test (Zar, 1984) was executed to test the null hypothesis that the frequency of the species associated to *C. criuva* was equal to their frequency of occurrence on the environment. One year later, the sites of recruitment were also surveyed and the frequency of each plant species was recorded as described above for each seedling. In the same period, survival of the established individuals was evaluated and a chi-square analysis or a Fisher's exact test (Zar, 1984) was performed to identify differences in mortality between opens areas, patches of shrubs, bromeliads and humid slacks.

Experiments on germination and survival

Mature fruits were collected at the time of their natural fructification (during summer, in January 2009). The fruits are globular capsules that dehisce to expose five diaspores, each one containing 0-17 seeds enveloped by a red aril (Passos and Oliveira, 2002). The aril that covers the diaspores was removed so that the seeds could be individualized. Twenty seeds were disposed uniformly in each one of the twenty plots (0.5m x 0.5m). The plots were divided equally in five replicates of four treatments: (i) open areas, (ii) beneath the canopy of *Guapira opposita* (Vell.) Reitz (Nyctaginaceae) (the most frequent species of shrub encountered associated with *C. criuva*), (iii) near a humid slack and (iv) inside a specimen of the tank bromeliad *Vriesea friburgensis* Mez (Bromeliaceae). In the bromeliad, seeds were placed inside the rosette, uniformly distributed in the third and forth concentric circle of leaves. Germination rate was measured in laboratory conditions with the same amount of seeds and replicates. In order to measure the germination rate, each plot was observed monthly and maximum germination was recorded. To facilitate reading, hereafter the treatments will be referred to as "open area", "shrub", "humid slack" and "bromeliad". Both the shrub and the bromeliad are not found in humid slacks (Guimaraes, 2006). A Generalized Linear Model (GLM) was used to detect the effect of the treatments on germination compared to the open area. Error distribution was chosen accordingly to the lowest AIC (Akaike Information Criteria). Analysis were made using R version 2.7.2 (R Development Core Team, 2008).

Additionally, seedlings were collected under the canopy of reproductive *C. criuva*, on April 2009, and transplanted in number of twenty seedlings per plot. Five plots were set for each of the four treatments described above. A control was created in the laboratory and watered daily in order to account for deaths due to transplant stress. Only seedlings with two cotyledons and approximately 3cm height were selected. Censuses of the surviving seedlings occurred once a month in the course of six months, when all remaining seedlings were removed. Their biomass and height was measured (using a digital paquimeter with 150mm/6” accuracy) and the number of leaves counted.

Survival curves were constructed using the Kaplan-Meier method. Survival data were analyzed using Cox Proportional-Hazard model for covariate analysis of censored data. The underlying assumption of the model is that there is a baseline hazard function that is modified multiplicatively by covariates (in this case the treatments). Diagnostics for proportional hazards were based on the scaled Schoenfeld residuals; while the effect of influential cases and nonlinearity were assessed with differences in beta (Dfbeta) and Martingale-residuals, respectively (Schoenfeld, 1980; Puterman, 1988; Therneau et al., 1990). Efron’s approximation to the risk set permutations on tied data was used (Fox, 2002). In this study, the time when the individuals were last observed alive was considered the time of death. For that reason, the estimates of survival times will be somewhat conservative. Since nonparametrical survival analysis cannot explicitly incorporate information from replication, seedlings were pooled across replicates, totalizing 100 individuals per treatment. Data analysis was performed using the “survival” package (Therneau and Lumley, 2008) in R version 2.7.2 (R Development Core Team, 2008).

Environmental conditions

Abiotic conditions were examined in the summer (February 2009). Measurements were made on five replicates of each treatment (open area, shrub, humid slack and bromeliad), from 10:30 to 12:00, during Summer. Soil temperature was determined using a thermometer inserted 1.5 cm into the sand. Light intensity was measured with a light meter (Extech Instruments 401025) placed at soil level or inside the bromeliads. Soil cores were taken in each place where the other measurements were made. Soil moisture was assessed by drying 20g of soil at 100^oC until the weight stabilized and calculating the difference between fresh and dry weight. Since tank bromeliads are filled with water and contain no soil, moisture in this environment was considered to be 100%. The soil organic matter content was determined as the loss of mass upon ignition (550°C, 2h). This measurement was not performed for the bromeliad because there was no soil to be collected. Also here, Generalized Linear Models were used to analyze data, comparing the results of the treatments to those obtained in open areas.

Results

Spatial association

Results revealed that the species observed associated to *C. criuva* do not coincide to those registered in the systematic sampling (Figure 1). Species that contributed the most to this differentiation were *Smilax campestris* Griseb. (Smilacaceae), *Vitex megapotamica* (Spreng.) Moldenke (Lamiaceae), *Guapira opposita* and *Gaylussacia brasiliensis* (Spreng.) Meisn. (Ericaceae).

In fact, the species most commonly associated with *C. criuva*. was *G. opposita*, followed by *V. megapotamica*, *S. campestris, G. brasiliensis* and *Vriesea friburgensis.* Their frequency of occurrence associated to *C. criuva* was 35.8%, 35.4%, 34.4%, 32.6% and 26.0%, respectively. Apart from the bromeliad *V. friburgensis* and from *S. campestris*, which is a climbing plant usually associated to woody plants, all the mentioned species are shrubs. When compared to the systematic sampling, most species had contrasting results. *G. opposita* was much less frequent (0.7%; χ^2=118.811; p<0.001) in the systematic sampling than in association to *C. criuva*, as well as *V. megapotamica* (7.3%; χ^2=71.680; p<0.001), *G. brasiliensis* (5.2%; χ^2=70.621; p<0.001) and *V. friburgensis* (1.7%; χ^2=71.129; p<0.001). The complete list, with the frequencies of all species found in the study, can be seen in appendix 1.

A great part of the individuals surveyed (45.3%) (n=301) was associated with some species of shrub and/or was found inside a vegetation island; 23.7% were associated only with *V. friburgensis* (outside vegetation islands) and 31.0% were not associated with either (10.7 % located on open areas and 20.3% near humid slacks). Mortality, however, was greater in the presence of shrubby neighbors, where 11.7% of the individuals died (n=137). On humid slacks and inside bromeliads, 5.0% (n=61) and 4.2% (n=71) of the individuals died, respectively. No deaths were observed in open areas (n=32). Statistical difference was observed only between the open area and the shrubs (Fisher’s exact test, p<0.05).

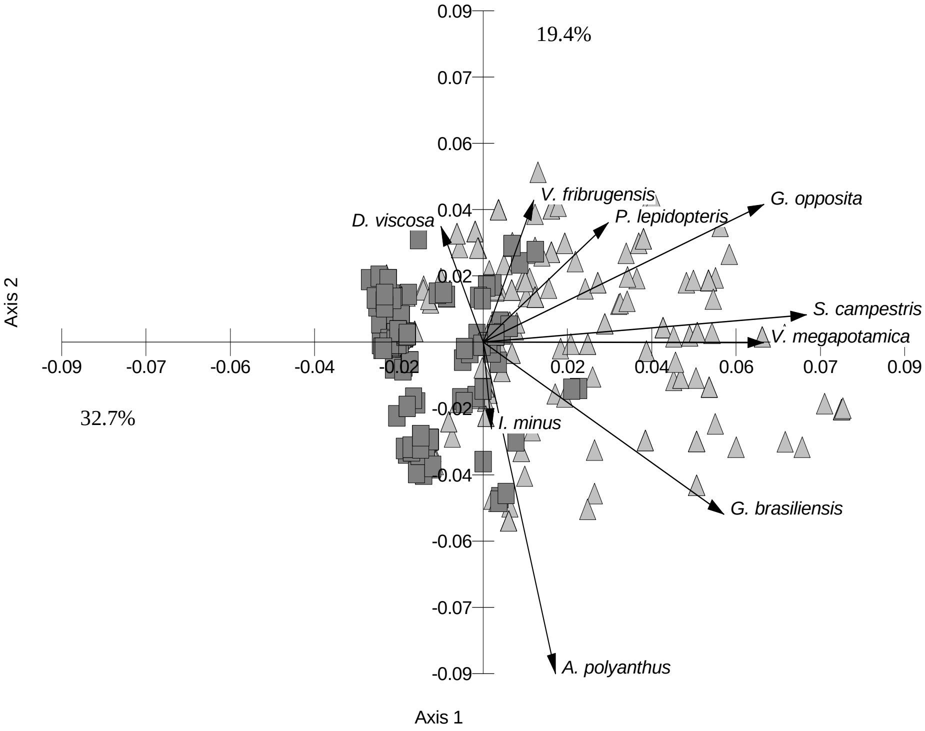

Figure 1. Ordination (PCA) species-samples diagram. Plots are displayed as triangles (samples with *C. criuva*) and rectangles (random sampling). More information on the species can be seen in Appendix 1

In one year, 194 individuals were recruited. Seedling recruitment occurred mainly beneath shrubs (n=184; 94.9%). One (0.5%) recruited inside a bromeliad and nine (4.5%) recruited on open areas. However, all of those recruiting in open areas were clones. The most common species under which seedlings recruited were *V. megapotamica*, *C. criuva*, *Polypodium lepidopteris* (Langsdorff & Fischer) Kunze (Polypodiaceae), *V. friburgensis* and *G. opposita.*

Environmental conditions

Substrate moisture was significantly different from open areas in all other three treatments (Figure 2a). In open areas, the percentage of water was close to zero. Probably linked to these results, substrate temperature was the lowest inside bromeliads, followed by shrubs and humid slacks (Figure 2b). Incidence of light was significantly lower only under the canopy of shrubs, but in humid slacks and bromeliads a tendency to reduction on the incidence of light could be noticed (Figure 2c). Organic matter content also differed only under the shrub, in spite of the great variation found in this treatment (Figure 2d).

Experiments on germination and survival

Germination of seeds was low in all sites, as well as in laboratory conditions, and nil in open areas (Table 1). Hence, there was no difference in seed germination among treatments ($p>0.05$). Nevertheless, the survivorship curves were different in all cases (Figure 3, Table 2) No seedlings survived the first month in open areas. Mortality in the first month was very high, probably due to transplant stress, since the same pattern was observed in the laboratory, where, on average, 2.8 (Std deviation =2.5) seedlings survived the first month. Overall increment in survival was stronger in humid slacks and weaker beneath *G. opposita* (Table 2). At the outset, most surviving seedlings were inside bromeliads. However, this initial strong positive effect decreased gradually with time, what also happened to the shrubs. In humid slacks, though, a steady rate of survival was disrupted by a considerable mortality observed between September and October.

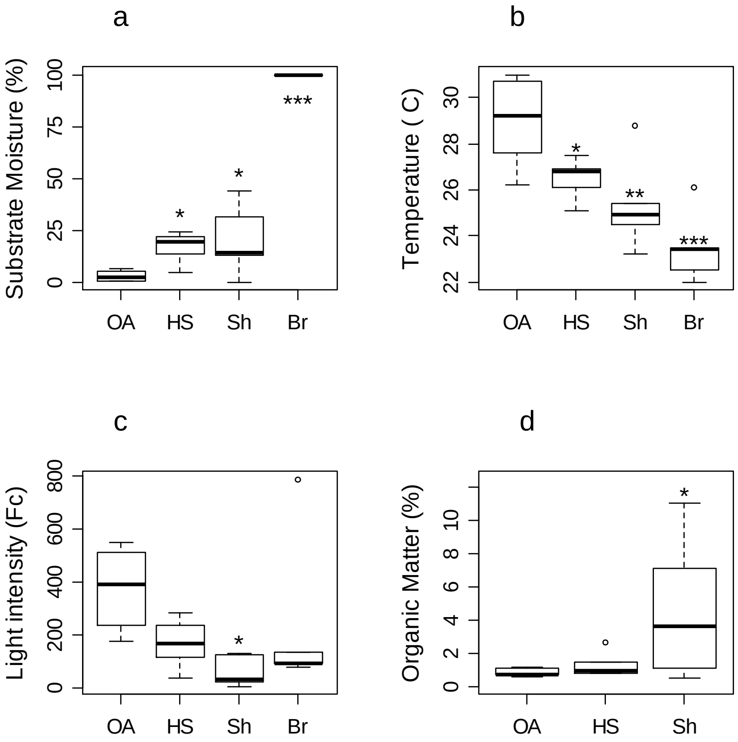

Figure. 2. Abiotic conditions in each treatment. (a) Substrate moisture (%), (b) Substrate Temperature (^{o}C), (c) Light intensity (Fc), (d) Organic Matter (%). OA= Open area, HS= Humid Slack, Sh= Beneath shrub, Br= Bromeliad. Central lines represent medians and boxes represent first and third quartiles. Whiskers represent 1.5 times the extent of the boxes (3Q-1Q) plus the value of the first and third quartile, for the lower and upper whisker, respectively. Circles represent outliers. Asterisks show the results of the generalized linear models, and represent significant statistical difference between each treatment and the open areas. *Significant at 5%; **Significant at 1%; ***Significant at 0,1%.

Table 1. Amount of germinated seeds of *Clusia criuva* in each treatment and in laboratory conditions. Mean and standard deviation per plot (n=5) are shown. Twenty seeds were placed in each plot.

Treatment	Germinated seeds	
	Total	Mean (SD)
Open Area	0	0 (0)
Humid Slack	2	0.4 (0.5)
Shrub	7	1.4 (1.8)
Bromeliad	4	0.8 (1.9)
Laboratory	14	4.8 (2.1)

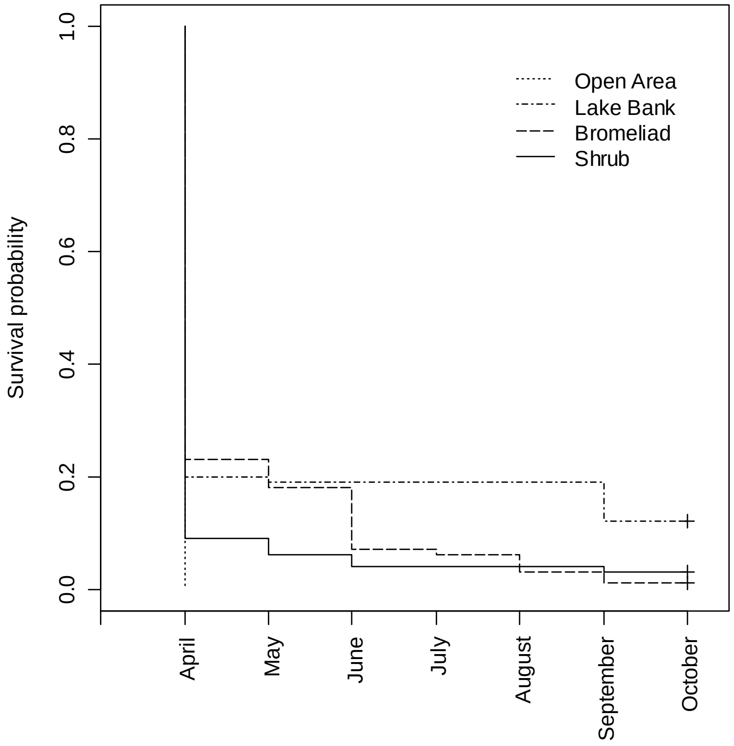

Figure 3. Survival curves of *Clusia criuva* seedlings (n=100) for each treatment. The x-axis represents the months when seedlings were last seen alive (Kaplan-Meier estimator).

Table 2. Results of Cox Proportional Hazard Model to identify the effect of treatments on *Clusia criuva* seedling survival compared to open areas. *Significant at 5%; **Significant at 1%; ***Significant at 0,1%.

Treatment	Hazard Ratio	95% Confidence Interval
Humid Slack	0.497***	0.396-0.671
Shrub	0.758***	0.453-0.801
Bromeliad	0.602***	0.572-1.005

Growth and final number of leaves was similar among treatments (Table 3). Biomass, though, was much smaller inside bromeliads, and the highest value found in bromeliads was smaller than the minimum values from the other treatments. Beneath *G. opposita*, biomass had an intermediate value and the greatest biomass was found in humid slacks.

Table 3. Number of *Clusia criuva* surviving seedlings and height, number of leaves and biomass of individuals per treatment after six months. Mean (min-max).

Treatment	Number of survivors	Height (cm)	Number of leaves	Biomass (g)
Open Area	0	–	–	–
Humid Slack	12	4.2 (2.3- 5.2)	4.2 (3-6)	36 (27-51)
Bromeliad	2	5.2 (4.8-5.8)	3 (2-4)	9 (8-10)
Shrub	3	4.7 (4.1-5.1)	4 (2-6)	28 (18-41)

Discussion

As already thoroughly explored in literature, positive spatial association, such as the one found between *C. criuva* and shrubby species or the bromeliad, can be an evidence of facilitation, since the beneficiated species will recruit preferably under the benefactor (Valiente-Banuet et al., 1991; Haase et al., 1996; Tewksbury and Lloyd, 2001; Callaway et al., 2000; Tirado and Pugnaire, 2005). Nonetheless, it can also represent spatial heterogeneity of resources and plants may be actually competing at a patch scale for resources distributed nonuniformly (Tirado and Pugnaire, 2003; Michalet, 2006). For that reason field experiments are required. Both recruited seedlings and established individuals of *C. criuva* were frequently associated to some species of shrub, what suggests the occurrence of positive interactions. Furthermore, survival of transplanted seedlings was improved under *G. opposita* in comparison to open areas. The canopy of *G. opposita* diminished incidence of light and soil temperature and also increased organic matter and water content. Indeed, amelioration of microclimatic conditions has been reported as one of the main mechanisms of facilitation, especially in extreme environments (Franco and Nobel, 1989; Callaway, 1995; Armas and Pugnaire, 2005). In coastal dunes, bare sand can reach temperatures as high as 70°C during mid-summer at the peak of radiation, what makes germination impossible for most species (Scarano, 2002). Besides shadow, canopies provide litter, whose slow decomposition adds nutrients to the soil and increases humidity, tempering limiting factors typical of this kind of environment (Lichter, 2000; Zaluar and Scarano, 2000). Enhancing in survival and establishment of seedlings due to the presence of shrubs has been seen in other coastal sand dunes. Martínez (2003) has detected the positive influence of the early colonizer *Chamaecrista chamaecristoides* on the establishment of the late colonizer grasses *Shizachyrium scoparium* and *Trachypogon plumosus* on the coast of the gulf of Mexico. Another study showed that the shrub *Myrica pensilvanica* beneficiated two herbaceous sand dune species through soil enrichment (Shumway, 2000).

Besides seed and seedling desiccation, limited seed dispersal can also constrain colonization by late-successional species (Day and Wright, 1989; Lichter, 2000). On sand dunes, most sites are inappropriate for seed germination and the accumulation of seeds on places that favor their establishment can be an important mechanism of facilitation (Franks, 2003). As showed by experimental results, germination, while low, could only happen in association to another species or in humid slacks. Since all seeds are produced outside the study area and considering that *C. criuva* is dispersed primarily by birds (Passos and Oliveira, 2002), shrubs and bromeliads could work as bird perches accumulating these seeds and avoiding their loss to open areas, where germination would not be possible. Birds were often observed on inflorescences of *V. friburgensis* and on the branches of *G. opposita*. Joy and Young (2002) had already determined that positive interactions among two woody species could be mediated through the non-random distribution of fleshy seeds by perching birds or through increased seedling survival. All the most common shrub species (*G. opposita*, *V. megapotamica* and *G. brasiliensis*) have fleshy fruits, what could attract seed dispersers. However, to confirm this hypothesis, studies that analyzed seed rain under these species and compared them to open areas would be necessary.

Regarding all of the parameters measured, seedlings were more successful in humid slacks, possibly due to the lower environmental severity in comparison to open areas. These results are supported by the SGH (Bertness and Callaway, 1994). Even though the two degrees of environmental severity tested in this experiment do not constitute a gradient of stress, it was possible to notice that a benefactor is indispensable for the establishment of seedlings in dry open areas, what did not happen in the milder environment of the humid slacks. As explained by Butterfield (2009), some species can be obligate beneficiaries within the most severe part of their distribution and be facultative beneficiaries in more favorable environments. Therefore, facilitation led to the expansion of the realized niche (Bruno et. al., 2003) of *C. criuva*, allowing the species to colonize greater areas than what would be possible in the absence of interspecific interactions. Nonetheless, it was perceived a size-dependent decrease in the importance of associations to *C. criuva*, given that many of the established individuals were found isolated in dry areas. In fact, considering only survival of established individuals, the performance of those in isolation was better than of those associated to other species, what could indicate an ontogenetic shift from facilitation to competition (Miriti, 2006). Although seedlings need a nurse plant to survive in drier areas, established individuals are able to endure in isolation. In these cases, the *C. criuva* individuals may have outcompeted their initial benefactors, since they are not present anymore. Similar results were already obtained by several studies (e.g. Anderson et al., 2001, Valiente-Banuet et al., 1991; Gasque & García-Fayos 2004). These observations can be explained by the simultaneous occurrence of competition and facilitation and their delicate balance that may easily shift in response to environmental variability in space and time (Bertness and Callaway, 1994; Armas e Pugnaire, 2005; Callaway, 2007). It is this balance that determines the net effects of the nurse plants on the growth and survival of seedlings (Berkowitz et. al., 1995) and, ultimately, the structure and composition of plant communities (Armas and Pugnaire, 2005).

Other negative effects could be identified. The smallest biomass on seedlings under the shrubs indicates that the shadow was probably inhibiting photosynthesis, what could also explain the results obtained in the bromeliads. Bromeliads increased substantially survival of seedlings in the first month, probably because of water availability. Regardless, by the end of the experiment, seedlings transplanted to bromeliads had the lowest biomass in all three treatments. In drier environments, the net result of the interplay between facilitation and competition is only positive when the improvement of water availability exceeds the costs caused by lower light levels (Holmgren et al., 1997). Hence, the greatest success of seedlings in humid slacks could also be due to the virtual absence of competition. In these locations, where the scarce herbaceous vegetation is not able to shade the seedlings and the superficial groundwater increases water availability, the positive net result is clear. Under shrubs and inside bromeliads there was also a positive net result, since seedlings were able to survive.

Conclusions

While in moister areas, facilitation is not a requirement, positive interactions seem to enable *C. criuva* to colonize dry areas of coastal sand dunes. Seeds do not germinate and seedlings cannot establish in such areas without a benefactor, but, once established individuals are able to live in isolation, competition may become more important than facilitation in the adult stage. Most likely, mechanisms involved in the positive interactions are: increase in water availability, reduction of substrate temperature and improvement of seed dispersal. Shadow appeared to have a negative effect on seedling growth. Results depended of the species of the benefactors.

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Appendix 1. Relative frequencies of the plant species found in association with *C. criuva* and in the systematic sampling. FA: relative frequency in association with *C. criuva*. FS: relative frequency in the systematic sampling. Family classification was made accordingly to APG II (APG 2003). Results of the chi-square analysis or Fischer's exact test (when the expected value was zero) are shown. χ^2= NA (not applicable) when Fischer's exact test was used. *Significant at 5%

Family	**Species**	**Habit**	**FA (%)**	**FS (%)**	**χ2**	**p**
Anacardiaceae	*Lithraea brasiliensis* Marchand	Shrub	2.4	0.3	NA	0.6840
Apiaceae	*Centella asiatica* (L.) Urb.	Herb	0	0.7	NA	0.4991
Apocynaceae	*Oxypetalum tomentosum* Wight ex Hook. & Arn.	Herb	0	0.3	NA	1.0000
Asteraceae	*Achyrocline satureioides* (Lam.) DC.	Herb	0	0.3	NA	1.0000
	Baccharis sp	Herb	0	1.0	NA	0.2487
	Baccharis radicans DC.	Herb	0	0.3	NA	1.0000
	Eupatorium casarettoi (B.L.Rob.) Steyerm.	Shrub	2.8	7.3	6.137	0.0222*
	Noticastrum malmei Zardini	Herb	0	8.7	NA	0*
	Porophyllum ruderale (Jacquin) Cassini	Herb	0	0.3	NA	1.0000
	Pterocaulon sp.	Herb	1.7	2.1	0.093	1.0000
Blechnaceae	*Blechnum serrulatum* Rich.	Herb	2.4	0	NA	0.0151*
Bromeliaceae	*Vriesea friburgensis* Mez	Bromeliad	26.0	1.7	71.129	<0.0001*
Cyperaceae	*Androtrichum trigynum* (Spreng.) H. Pfeiff.	Herb	12.2	7.6	2.804	0.0940
	Cyperus cf. sesquiflorus (Torr.) Mattf. & Kük.	Herb	0	0.3	NA	1.0000
	Cyperus L.	Herb	1.4	3.5	1.830	0.1761
	Unidentified 1	Herb	0.7	0	NA	0.4991
	Unidentified 2	Herb	0	5.6	NA	0*

cont.

	Unidentified 3	Herb	0.3	0	NA	1.0000
Dryopteridaceae	*Rumohra adiantiformis* (Forster) Ching	Herb	2.8	0	NA	0.0074*
Ericaceae	*Gaylussacia brasiliensis* (Spreng.) Meisn.	Shrub	32.7	5.6	66.623	<0.0001*
Eriocaulaceae	*Actinocephalus polyanthus* (Bong.) Kunth	Herb	21.2	16.3	2.234	0.1650
Euphorbiaceae	*Alchornea triplinervia* (Spreng.) Müll. Arg.	Shrub	2.4	0	NA	0.0151*
Lamiaceae	*Vitex megapotamica* (Spreng.) Moldenke	Shrub	35.4	7.3	71.680	<0.0001*
Lauraceae	*Ocotea pulchella* (Nees) Mez	Shrub	2.4	0.3	NA	0.6840
Fabaceae - Fab.	*Desmodium adscendens* (Sw.) DC.	Herb	2.4	1.7	0.340	0.7705
	Sophora tomentosa L.	Shrub	0.7	0	NA	0.4991
	Stylosanthes viscosa (L.) Sw.	Herb	0	4.2	NA	0.0004*
Melastomataceae	*Tibouchina asperior* (Cham.) Cogn.	Herb	2.4	0	NA	0.0151*
	Tibouchina sp	Herb	2.8	1.0	2.317	0.2233
	Unidentified 1	Herb	1.4	0	NA	0.1237
Myrsinaceae	*Myrsine cf. parvifolia* A. DC.	Shrub	4.5	0	NA	0.0002*
	Myrsine cf. umbellata Mart.	Shrub	3.1	0	NA	0.0037*
	Myrsine coriacea (Sw.) R. Br. ex Roem. & Schult.	Shrub	0.3	0	NA	1.0000
Myrtaceae	*Eucalyptus* sp	Shrub	0	0.3	NA	1.0000
	Eugenia catharinae O. Berg	Shrub	2.4	0	NA	0.0151*
	Gomidesia palustris (DC.) Kausel	Shrub	7.6	0	NA	0*
	Unidentified 1	Shrub	0.3	0	NA	1.0000
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	Shrub	35.8	0.7	118.811	<0.0001*
Orchidaceae	*Epidendrum fulgens* Brongn.	Herb	2.1	3.5	1.029	0.4469
Pinaceae	*Pinus elliottii* Engelm.	Shrub	2.1	0	NA	0.0304*

cont.

Piperaceae	*Peperomia glabella* (Sw.) A. Dietr.	Herb	0	0.7	NA	0.4991
Poaceae	*Andropogon selloanus* (Hack.) Hack.	Herb	0.7	7.6	15.696	<0.0001*
	Andropogon sp	Herb	0	0.3	NA	1.0000
	Aristida circinalis Lindm.	Herb	4.5	0	NA	0.0002*
	Ischaemum minus J. Presl	Herb	12.5	4.9	9.658	0.0019*
	Panicum sp	Herb	0	1.4	NA	0.1237
	Paspalum sp1	Herb	0	2.8	NA	0.0074*
	Paspalum sp2	Herb	0.3	0	NA	1.0000
	Spartina ciliata Brongn.	Herb	0.7	10.1	NA	0.4991
	Unidentified 1	Herb	4.2	0	NA	0.0004*
	Unidentified 2	Herb	0	2.4	NA	0.0151*
	Unidentified 3	Herb	0	2.4	NA	0.0151*
	Unidentified 4	Herb	0	2.1	NA	0.0304*
	Unidentified 5	Herb	0	0.3	NA	1.0000
	Unidentified 6	Herb	0	0.3	NA	1.0000
Polypodiaceae	*Polypodium lepidopteris* (Langsdorff & Fischer) Kunze	Herb	21.9	2.1	53.495	<0.0001*
Rubiaceae	*Diodela radula* (Willd. & Hoffmanns. ex Roem. & Schult.) Delprete	Herb	5.6	4.2	0.601	0.5611
Sapindaceae	*Dodonaea viscosa* Jacquin	Shrub	10.8	15.6	2.971	0.1095
Smilacaceae	*Smilax campestris* Griseb	Climbing	34.4	3.8	87.018	<0.0001*

Considerações finais

Na restinga herbácea/subarbustiva do Parque Municipal das Dunas da Lagoa da Conceição, a população de *Clusia criuva* está em crescimento e provavelmente a colonização da área ainda está em fase inicial. A sobrevivência dos adultos, que se reproduzem clonalmente, tem a maior importância para a manutenção deste crescimento. No ano de estudo, o recrutamento de genetas, que dependeu totalmente de fontes externas de sementes, foi mais expressivo do que a produção de rametas. No entanto, este fenômeno parece ser irregular e depender de anos favoráveis, enquanto que a propagação clonal deve ser contínua, garantindo a estabilidade nos anos que a propagação por sementes não é possível.

Em áreas secas e abertas, desprovidas de vegetação as sementes de *C. criuva* não germinam e as plântulas não conseguem sobreviver. Por isso, a presença de plantas facilitadoras, que amenizam as condições abióticas, especialmente diminuindo a temperatura do substrato e aumentando a disponibilidade de água, são essenciais para o estabelecimento de novos indivíduos por semente. A existência desta interação positiva também ajuda a explicar o padrão de distribuição agregado encontrado em pequenas escalas. Provavelmente, as espécies facilitadoras formam núcleos ao seu redor, onde as condições são propícias ao estabelecimento de espécies menos resistentes, originando as moitas de plantas arbustivas (ilhas de vegetação) observadas na restinga. Espécies arbustivas foram as mais frequentemente encontradas em associação com *C. criuva*, mas a bromélia *Vriesea friburgensis* também merece destaque, pois comprovadamente aumenta a germinação das sementes e a sobrevivência das plântulas. O mesmo pode ser dito sobre a espécie arbustiva *Guapira opposita*. Estas espécies poderiam também estar agindo como poleiros, estimulando a deposição de sementes em sítios adequados à germinação.

Contudo, não só as interações positivas são responsáveis pelo recrutamento de novos indivíduos genéticos de *C. criuva*. A restinga na área de estudo é muito heterogênea, apresentando dunas semifixas, entremeadas por baixadas, ilhas de vegetação e corpos d’água. Sendo assim, apesar do estabelecimento de plântulas não ser possível em áreas abertas, as bordas de baixadas úmidas e alagáveis são ambientes propícios a este estabelecimento e espécies facilitadoras não são necessárias. O padrão agregado de distribuição também pode ser decorrente do tamanho reduzido destas áreas favoráveis.

Apesar da localização de indivíduos jovens ser limitada a pequenas áreas onde a densidade é alta, não foi observado um forte efeito de mortalidade dependente de densidade, visto que o padrão de distribuição espacial de plantas jovens e já estabelecidas é similar. Os adultos apresentam o mesmo padrão de distribuição dos indivíduos juvenis. Entretanto, os indivíduos já estabelecidos não precisam das mesmas condições que as plântulas, visto que muitos foram encontrados em áreas abertas e a mortalidade nestes locais foi menor quando comparada às moitas. Possivelmente, estes indivíduos se estabeleceram em áreas úmidas ou na presença de facilitadores, que podem ter sido eliminados posteriormente por competição.

Neste ambiente, as interações positivas parecem bastante importantes, especialmente para o estabelecimento de plântulas, apesar de alguns efeitos negativos poderem ser percebidos. Em estágios mais avançados, a competição pode ter mais relevância. É a combinação destas interações, positivas e negativas, que determina a sobrevivência e a distribuição das espécies e, consequentemente, a composição florística e o aspecto da paisagem.

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