UNIVERSIDADE ESTADUAL DE CAMPINAS

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INFLUÊNCIA DA VARIAÇÃO FISIONÔMICA DA VEGETAÇÃO SOBRE A COMPOSIÇÃO DE AVES FRUGÍVORAS NA MATA ATLÂNTICA

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Este exemplar corresponde à redação final da tese defendida pelo(a) candidato (a) Érica Hasui e aprovada pela Comissão Julgadora.

Wesley R. Silva

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Quantas são as tuas obras, Senhor!
Fizeste todas elas com sabedoria!
A terra está cheia de seres que criastes.
Cantarei ao Senhor toda a minha vida;
Louvarei ao meu Deus enquanto eu viver.
Seja-lhe agradável a minha meditação,
Pois no Senhor tenho alegria.
(Salmo 104: 24 e 34)

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RESUMO

Em função da devastação ímpar que as florestas tropicais vêm sofrendo, faz-se necessário um conhecimento mais aprofundado da organização das comunidades biológicas enfocando as interações interespecíficas entre as aves e as plantas. Embora este aspecto não seja considerado prioritário nas medidas de conservação da biodiversidade, é de extrema importância para manter comunidades frugívoras e garantir a persistência das interações entre as espécies.

A variação espacial e temporal das aves foi estudada em diferentes habitats conectados de Mata Atlântica, entre abril de 1999 e março de 2002, procurando enfocar as seguintes perguntas: 1) Quais fatores poderiam afetar a riqueza e a abundância de aves considerando a variação na estrutura da vegetação, diversidade florística e abundância de frutos no mosaico de habitats da Mata Atlântica? 2) Qual o efeito da variação espacial e temporal da abundância e da qualidade de frutos sobre a abundância de aves frugívoras? 3) Como variam os critérios de seleção dos frutos pelos frugívoros em relação à morfologia e ao conteúdo nutritivo do fruto. Qual seria o efeito da rigidez destes parâmetros sobre a riqueza de espécies de frutos consumidos?

Para responder tais perguntas, foram estabelecidas cinco unidades amostrais em cada tipo de habitat, cada uma consistindo de uma linha de redes para captura das aves com parcelas adjacentes a esta linha para obtenção de dados fenológicos e de estrutura e composição de espécies vegetais. A estrutura da vegetação foi caracterizada a partir de medições de altura total, altura de fuste, diâmetro à altura do peito e das freqüências das formas de vidas dos indivíduos no interior das parcelas. Em viagens mensais, as plantas no interior das parcelas foram vistoriadas quanto à presença de frutos maduros zoocóricos e as aves foram capturadas nas redes para a avaliação da dieta alimentar através do conteúdo das fezes. Simultaneamente foram realizadas observações diretas do comportamento alimentar das aves para registrar as interações entre as plantas e as aves. Todos os frutos ornitocóricos encontrados dentro ou fora das parcelas foram caracterizados morfologicamente e em relação ao conteúdo nutricional do fruto.

Os resultados indicam que as aves exibiram diferenças específicas no grau de tolerância em relação a este conjunto de variáveis bióticas. Os insetívoros e alguns frugívoros mais generalistas de sub-bosque (E-OI e U-FI) foram mais sensíveis às variações na estrutura da vegetação e no hábito de vida das plantas. Por outro lado, a composição de plantas foi mais importante para os frugívoros mais especialistas de copa (C-FI, E-FI e C-LF) e provavelmente para os granívoros. Os nectarívoros foram os mais tolerantes a estas variáveis, não exibindo qualquer correlação significativa.

As comunidades de aves foram caracterizadas por apresentar um equilíbrio dinâmico com flutuações temporais de composição de espécies e de abundância de indivíduos, parâmetros estes correlacionados com as mudanças na disponibilidade de alimento. Isto sugere que muitas espécies de aves parecem movimentar-se entre os habitats. Este comportamento pode ser favorecido pelas flutuações assincrônicas na abundância de frutos e nas diferenças das médias mensais das características morfológicas e nutrionais dos frutos produzidos entre os habitats.

No geral, as aves apresentam uma dieta alimentar diversificada em termos de composição de espécies de frutos; mas, ao mesmo tempo, são seletivos quanto às características morfológicas e nutricionais dos frutos consumidos. A especialização das aves quanto ao critério de seleção morfológica dos frutos pode estar associado ao tamanho corpóreo da ave, porque as espécies de aves menores tenderam a apresentar uma menor amplitude morfológica de nicho. Em relação as características selecionadas, as aves maiores tenderam a consumir frutos com sementes grandes, ao passo que as aves menores selecionaram os frutos com sementes pequenas. A riqueza de espécies de frutos presentes na dieta não esteve relacionada com o tamanho corpóreo das aves e nem com o grau de especialização das aves em relação às características morfológicas e/ou nutricionais dos frutos consumidos.

ABSTRACT

Due to the alarming rate of deforestation in tropical forests, a better understanding on the organization of biological communities is needed, specifically regarding the interactions between birds and plants. Although this aspect is not often included among the top priorities for biodiversity conservation, it must be considered an important of effort in the attempts to maintain functional communities and to guarantee the continuing of species interactions over time.

The spatial and temporal variation on bird abundance was studied in different habitats of Atlantic Forest, from April 1999 to March 2002, in order to answer the following questions: 1) What of these factors could more affect bird abundance and species richness in the Atlantic Forest habitats: vegetation structure, plant species composition or fruit abundance? 2) What are the effects of the temporal and spatial variation of the fruit abundance and quality on frugivorous bird abundance? 3) How do frugivorous birds selected fruits in relation to morphology and nutritional composition? Is there any relationship between fruit species richness and fruit morphology or fruit quality?

To answer these questions, five sample units were set in each habitat, each consisting of one line of mist nets associated with three adjacent plots where bird captures were conducted along with the recording of phenological and vegetational structure data. The vegetation structure was characterized by the following variables: total height, lower crown height, diameter at breast height and frequencies of plant habits. In monthly field trips, plants inside the plots were examined for the presence of zoochorous ripe fruits and birds were mist-netted. Information about interactions between birds and plants were obtained by the occurrence of seeds in fecal samples of captured birds, as well as by recording their feeding behavior. All ripe fruits found in each habitat were measured and their pulp collected for chemical analyses.

Results indicate that bird communities were sensitive to the variation in floristic and vegetation structure among habitats and showed particular preference for some specific positions along a gradient of

environmental conditions, with different functional groups or guilds being differentially tolerant to variations in these conditions. Vegetation structure and plant habit seem to have a stronger influence on insectivores and some generalist frugivores/insectivores of understory (E-OI e U-FI), while plant composition plays a more important role for other specialist frugivore of canopy (C-FI, E-FI e C-LF) and probably for seed-eaters. Nectarivores showed high tolerance of these vegetation variables.

We found a high spatial heterogeneity among habitats associated with differences in plant species composition. The habitats also had an asynchronous temporal pattern in fruit abundance and significant differences on monthly means of morphological and nutritional traits of fruits over vertical strata and among habitats. At the landscape level, these patterns suggest that, as a whole, the mosaic of different habitats can be seen as a non-seasonal unit, where the different patches complement each other in fruiting phenology. These conditions may affect bird communities because they were characterized by dynamic systems with temporal fluctuation in abundance and bird species composition. Significant correlation among fruit variables and bird abundance suggest that some bird species move into or out of habitats according to more favorable fruit availability.

In general, birds eat a high diversity of fruit species; but at the same time, they show clear preferences and select fruits according to morphological and nutritional traits. The fruit morphological specialization may be associated with bird size, because the smaller birds had the smaller morphological niche breadth. In relation of morphological fruit selection, the larger birds selected fruits with larger seed mass and size and while the smaller birds selected fruits with small seeds mass and size. In contrast with the high morphological specialization found in most birds, the general pattern observed for nutritional traits is a generalist feeding strategy. It seems that the strong nutritional imbalance characterizing the pulp of most fruit species should force frugivores to adopt a mixed-species diet with high variation on nutritional content in order to get a balanced input of energy, protein, vitamins, and minerals. The bird species showed a wide flexibility concerning the nutritional fruit traits but not with the same nutritional requirement. The fruit species richness consumed by birds was not associated with bird size and neither with morphological and/or nutritional traits of fruit consumed.

INTRODUÇÃO GERAL

Nos últimos anos, biólogos e conservacionistas voltaram seus olhos com maior atenção para as florestas tropicais, por duas razões principais. Primeiro, embora esses habitats cubram apenas 7% da superfície terrestre, eles contêm mais da metade das espécies da biota mundial. Segundo, as florestas estão sendo destruídas tão rapidamente que elas provavelmente desaparecerão dentro do próximo século, levando com elas centenas de milhares de espécies à extinção (Viana e Tabanez 1996, Wilson 1997).

A Mata Atlântica (*sensu lato*), que originalmente recobria boa parte da região costeira do Brasil, avançando para o interior em alguns trechos, acha-se hoje bastante fragmentada ao longo de sua área de distribuição, tendo sido reduzida a menos de 8% da sua cobertura original e restrita às áreas de difícil acesso (Ministério do Meio Ambiente 1999). De fisionomia bastante variada, geralmente condicionada por fatores climáticos, edáficos e topográficos, a Floresta Atlântica representa ainda hoje um dos maiores pólos extra-amazônicos de diversidade biológica, o que a coloca entre as áreas prioritárias para a implantação de medidas conservacionistas, uma vez que muitas espécies de plantas e animais são endêmicas da região e a permanência futura destas espécies em pequenos habitats fragmentados é seriamente questionável (Terborgh 1992).

Das 687 espécies de aves registradas por Parker *et al.* (1996), mais de 200 espécies são endêmicas (Goerck 1997). Apesar de relativamente bem conhecida a distribuição espacial destas espécies, os fatores que limitam suas distribuições precisam ser melhor esclarecidos para que sejam considerados nas medidas de conservação (Greenwood 1992). Os processos relacionados com a distribuição das espécies tem chamado a atenção de muitos pesquisadores, tanto em áreas tropicais como temperadas (Karr and Roth 1971, Terborgh 1977, Hino 1985, Allegrini 1997, Goerck 1999). Neste trabalho abordei a influência dos fatores bióticos na distribuição das espécies em nível de guilda. Além disto, analisei a organização das comunidades biológicas enfocando as interações das aves frugívoras com as plantas. Embora estes aspectos não sejam considerados prioritários nas medidas de conservação da biodiversidade, são de extrema importância para manter a viabilidade das comunidades e garantir a persistência e evolução das interações entre as espécies (Terborgh 1992, Meyer 1997, Thompson 1997). Assim, foram analisados os seguintes fatores:

1) Complexidade estrutural do habitat

Muitos estudos sugeriram que a estrutura da vegetação (*p.e.,* altura da vegetação, densidade de árvores, estratificação da vegetação, número de espécies vegetais sobrepostas nos estratos) (Cody 1981, Wiens 1989) constitui um dos fatores preponderantes na determinação do número de espécies de aves em nível local. Esta afirmação está baseada nas correlações estabelecidas entre o grau de complexidade estrutural do habitat, p. e., ao longo de algum gradiente ambiental, e a diversidade de espécies de aves (MacArthur *et al.* 1962, Allegrini 1997, Goerck 1999). Assim, muitos estudos foram realizados comparando a diversidade e a abundância de aves em habitats com estruturas vegetais distintas (Finch 1989, Blake *et al.* 1990, Graham 1990, Robertson e Hackwell 1995, Aleixo 1999).

No entanto, segundo Terborgh (1985), os aspectos estruturais têm sido super valorizados nos estudos de seleção de habitat pelas aves, enquanto outros fatores são negligenciados (*p.e.,* condições microclimáticas, substrato apropriado para o forrageamento, recurso alimentar, local de nidificação, excessivo grau de competição, predação e parasitismo), talvez pela maior dificuldade de mensuração, mas que podem ser igualmente importantes e deveriam ser considerados simultaneamente nos estudos.

2) Recurso alimentar

A disponibilidade de recurso alimentar é um importante aspecto na seleção do habitat, mas que tem recebido relativamente pouca atenção (Terborgh 1985). Os estudos relacionados ao recurso alimentar dão ênfase aos padrões de variação espacial e temporal e os relacionam com a riqueza de espécies, movimento e flutuação sazonal na abundância de aves em nível de espécies e de guildas (Levey 1988, Poulin *et al.* 1994, Jordano 1995, Develey e Peres 2000, Gomes 2001).

No geral, as comunidades tropicais apresentam variações espaciais e temporais de disponibilidade de frutos que afetam diretamente os frugívoros (Goerck 1997). Eles podem responder por meio de uma mudança na dieta, em uma mudança na área de ocupação ou por meio de migração (Van Schaik *et al.* 1993).

A mudança na dieta em período de escassez de alimento é uma adaptação menos drástica e foi observada em muitos animais. Durante estes períodos muitos animais acabam se sujeitando a uma dieta com valor nutritivo mais baixo (p.e., bambus, folhas, pétalas), ou alimentos altamente protegidos que demandam mais tempo na sua manipulação (p.e., palmeiras, nozes), ou com presença de compostos secundários que limitam a quantidade de alimento ingerida (p.e., frutos imaturos), ou ainda que estão distribuídos difusamente no ambiente e que necessitam mais tempo para sua procura (p. e., néctar, insetos) (Galetti *et al.* 2000, Renton 2001, McKnight e Hepp 1998).

Muitos animais tropicais expandem sua área de vida, ou deslocam o uso de seus habitats de modo a se ajustar às variações de disponibilidade de alimento. A amplitude de variação dos deslocamentos varia em escala espacial. Eles podem mover-se dentro de um mesmo habitat constituído por mosaicos com diferenças de disponibilidade de alimento (Leighton e Leighton 1983, Levey 1988, Blake e Loiselle 2000).

As migrações altitudinais foram documentadas em muitas florestas tropicais e são especialmente importantes para as espécies que dependem das plantas como recurso alimentar (fruto e néctar). Estes movimentos devem ser favorecidos pelas variações temporais nos picos de frutificação das espécies ao longo do gradiente altitudinal (Loiselle 1987, Loiselle e Blake1991).

3) Variações interespecíficas na seleção de fruto

As características dos frutos que são relevantes aos frugívoros, incluem: os aspectos morfológicos (*p.e.* tamanho, número e tamanho das sementes, massa relativa de polpa em relação à massa de sementes), conteúdo nutritivo (quantidade relativa de lipídio, proteína, carboidratos, sais minerais) e metabólitos secundários (Moermond e Denslow 1985, Wheelwrigth 1985, Sun *et al.* 1997, Levey e Cipollini 1998, Witmer e Soest 1998). Estas características, apesar de não se relacionarem diretamente com a seleção do habitat por serem características específicas das espécies de plantas, são chaves para determinar a qualidade do habitat para os frugívoros.

Caso a distribuição de espécies de plantas no habitat reflita em algum padrão associado às características dos frutos, é bem plausível que isto influencie na seleção do habitat, como foi verificado no vale de Guadalquivir, na Espanha (Herrera 1985). Neste local, o diâmetro médio dos frutos variou significativamente com a elevação ao longo do vale, com os frutos menores nas baixadas e os maiores nas partes mais altas. Este gradiente altitudinal coincide paralelamente com a variação na largura média do bico das espécies de aves frugívoras do local.

OBJETIVOS GERAIS

Foi estudada a variação espacial e temporal das aves em diferentes habitats conectados de Mata Atlântica no Parque Estadual Intervales, procurando abordar as seguintes perguntas:

1) Quais fatores poderiam mais afetar a riqueza e a abundância de aves considerando a variação na estrutura da vegetação, diversidade florística e abundância de frutos no mosaico de habitats da Mata Atlântica?

2) Qual o efeito da variação espacial e temporal da abundância e da qualidade de frutos sobre a abundância de aves frugívoras?

4) Como variam os critérios de seleção dos frutos pelos frugívoros em relação à morfologia e ao conteúdo nutritivo do fruto? Qual seria o efeito da amplitude morfológica e nutricional do nicho das aves sobre a riqueza de espécies de frutos consumidos?

REFERÊNCIAS CITADAS

ALEIXO, A. 1999. Effects of selective logging on a bird community in the Brazilian Atlantic forest. *Condor* 101(3): 537-548.

ALLEGRINI, M. F. 1997. *Avifauna como possível indicador biológico dos estádios de regeneração da Mata Atlântica*. MSc. Thesis, University of São Paulo, São Paulo, Brazil. 161 p.

BLAKE, J. G. and LOISELLE, B. A. 2000. Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. *Auk* 117 (3): 663-686.

BLAKE, J. G., STILES, F. G., and LOISELLE, B. A. 1990. *Birds of La Selva Biological Station: habitat, use, trophic composition, and migrants*. Pp. 161-182. *In*: Gentry, A. (Ed.). Four Neotropical Rainforests. Yale University Press, New Haven.

CODY, M. L. 1981. Habitat selection in birds: The roles of vegetation structure, competitors and productivity. *BioScience* 31: 107-113.

DEVELEY, P. F. and PERES, C. A. 2000. Resource seasonality and the structure of mixed species bird flocks in a coastal Atlantic forest of southeastern Brazil. *Journal of Tropical Ecology* 16: 33-53.

FINCH, D. M. 1989. Habitat use and habitat overlap of riparian birds in three elevational zones. *Ecology* 70 (4): 866-880.

GALETTI, M., LAPS, R., and PIZO, M. A. 2000. Frugivory by Toucans (Ramphastidae) at two altitudes in the Atlantic Forest of Brazil. *Biotropica* 32(4b): 842-850.

GOERCK, J. M. 1997. Patterns of rarity in the birds of the Atlantic Forest of Brazil. *Conservation Biology* 11(1): 112-118.

GOERCK, J. M. 1999. Distribution of birds along an elevational gradient in the Atlantic forest of Brazil: implications for the conservation of endemic and endangered species. *Bird Conservation International* 9: 235-253.

GOMES, V. S. M. 2001. *Variação espaço-temporal de aves frugívoras no sub-bosque e chuva de sementes em um trecho de Mata Atlântica no Estado de São Paulo*. MSc. Thesis, University of Campinas, São Paulo, Brazil. 82p.

GRAHAM, G. L. 1990. Bats versus birds: comparisons among Peruvian volant vertebrate faunas along an elevational gradient. *J. Biogeography* 17: 657-668.

GREENWOOD, J. J. .D. 1992. Understanding bird distributions. *Tree* 7(8): 252-253.

HERRERA, C. M. 1985. *Habitat-consumer: Interactions in frugivorous birds*. Pp. 341-365. *In*: Cody, M. L. (Ed.). Habitat selection in birds (Physiological ecology). Academic Press Inc.

HINO, T. 1985. Relationships between bird community and habitat structure in shelterbelts of Hokkaido Japan. *Oecologia* 65(3): 442-448.

JORDANO, P. 1995. Spatial and temporal variation in the avian-frugivore assemblage of *Prunus mahaleb*: patterns and consequences. *Oikos* 71: 479-491.

KARR, J. R. and ROTH, R. R. 1971. Vegetation structure and avian diversity in several new world areas. *American Naturalist* 105(945): 423-435.

LEIGHTON, M. and LEIGHTON, D. R. 1983. *Vertebrate responses to fruiting seasonality within a Bornean rain forest*. Pp. 181-196. *In*: Sutton, S. L., Whitmore, T. C. and Chadmuck, A. C. (Ed.) Tropical rain forest: Ecology and management. Blackwell Sci. Publ. , London.

LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58(4): 251-269.

LEVEY, D. J. and CIPOLLINI, M. L. 1998. A glycoalkaloid in ripe fruit deters consumption by cedar waxings. *Auk* 115(2): 359-367.

LOISELLE, B. A. 1987. Migrant abundance in Costa Rican lowland forest canopy. *Journal of Tropical Ecology* 3:163-168.

LOISELLE, B. A and BLAKE, J. G. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72(1): 180-193.

MAcARTHUR, R. H., MAcARTHUR, J. W., and PREER, J. 1962. On bird species diversity II. Prediction on bird censuses from habitat measurements. *American Naturalist* 96:167-174.

MCKNIGHT, S. K., and HEPP, G. R. 1998. Foraging-niche dynamics of gadwalls and American coots in winter. *Auk* 115(3): 670-683.

MEYER, J. L. 1997. *Conserving ecosystem function*. Pp. 136-145. *In:* Pickett, S. T. A.; Ostfeld, R. S.; Shachak, M.; Likens, G. E. (Eds.). The ecological basis of conservation: heterogeneity, ecosystems and biodiversity. International Thomson Publishing.

MINISTÉRIO DO MEIO AMBIENTE 1999. *Diretrizes para a política de conservação e desenvolvimento sustentável da Mata Atlântica*. Caderno n°13. Brasília, DF, Brasil.

MOERMOND, T. C, and DENSLOW, J. S. 1985. *Neotropical avian frugivores: patterns of behaviour, morphology, and nutrition with consequences for food selection*. Pp. 865-897. *In*: Buckley, P. A., Foster, M. S., Morton, E. S., Ridgely, R. S., Smith, N. G. (Eds.). Neotropical Ornithology. Ornithological Monographs. Vol. 36.

PARKER, T. A. III, STOTZ, D. F., and FITZPATRICK, J. W. 1996. *Ecological and distributional databases*. Pp. 115-436. *In:* Stotz D. F., Fitzpatrick J. W., Parker T. A. III, and Moskovits D. K. (Eds.). Neotropical Birds: Ecology and conservation. University of Chicago Press, Chicago.

POULIN, B., LEFEBVRE, G., and MCNEIL, R. 1994. Characteristics of feeding guilds and variation in diets of birds species of three adjacent tropical sites. *Biotropica* 26(2): 187-197.

RENTON, K. 2001. Lilac-crowned parrot diet and food resource availability: Resource tracking by a parrot seed predator. *Condor* 103(1): 62-69.

ROBERTSON, H. A., and HACKWELL, K. R. 1995. Habitat preferences of birds in serial Kahikatea *Dracrycarpus dacrydioides* (Podocarpaceae) forest of South Westland, New Zealand. *Biol. Conserv*. 71 (3): 275-280.

SUN, C., MOERMOND, T.C., and GIVNISH, T. 1997. Nutritional determinant of diet in three turacos in a tropical montane forest. *Auk* 114(2): 200-211.

TERBORGH, J. 1977 . *Bird species diversity on an Andean elevational gradient. Ecology* 58: 1007-1019.

TERBORGH, J. 1985. *Habitat selection in Amazonian birds.* Pp.311-338. *In*: Cody, M. L. (Ed.). Habitat selection in birds. Academic Press. New York.

TERBORGH, J. 1992. Maintenance of diversity in tropical forests. *Biotropica* 24 (2b): 283-292.

THOMPSON, J. N. 1997. *Conserving interaction biodiversity.* Pp. 285-293. *In*: Pickett, S. T. A.; Ostfeld, R. S.; Shachak, M.; Likens, G. E. (Eds.). The ecological basis of conservation: heterogeneity, ecosystems and biodiversity. International Thomson Publishing.

VAN SCHAIK, C. P., TERBORGH, J. W., and WRIGHT, S. J. 1993. The phenology of tropical forests: Adaptive significance and consequences of primary consumers. *Annu. Rev. Ecol. Syst.* 24: 353-377.

VIANA, V. M. and TABANEZ, A. A. J. 1996. *Biology and conservation of forest fragments in the Brazilian Atlantic Moist Forest.* Pp. 151-167. *In:* Schelhas, J. and Greenberg, R. (Eds.). Forest patches in tropical landscapes. Island Press. , Washington DC.

WHEELWRIGTH, N. T. 1985. Fruit size, gape width and the diets of fruit-eating birds. *Ecology* 66: 808-818

WIENS, J. A. 1989. *The ecology of birds communities*. Vol. 1. Foundations and patterns. Cambridge University Press, Cambridge. 539p.

WILSON, E. O. 1997. *A situação atual da diversidade biológica.* Pp. 3-24. *In*: Wilson, E. O. & Peter, F. M. eds. Biodiversidade. Editora Nova Fronteira, Rio de Janeiro.

WITMER, M. C., and VAN SOEST, P. J. 1998. Contrasting digestive strategies of fruit-eating birds. *Functional Ecology* 12(5): 728-741.

CAPÍTULO 1

BIRD COMMUNITY VARIATION ON DIFFERENT HABITATS IN ATLANTIC FOREST, BRAZIL

BIRD COMMUNITY VARIATION ON DIFFERENT HABITATS IN ATLANTIC FOREST, BRAZIL

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ABSTRACT

Between April 1999 and March 2002, birds and vegetation were sampled in four forest sites in southern São Paulo state, Brazil. One site was at secondary forest (SF) and three at primary forest, comprising three different physiognomies: bottom of valley (BV), middle slope (MS) and hilltop (HT). Birds were captured in mist nets, while vegetation structure, plant species composition and fruiting phenology were sampled in plots established along the nets' line. SF did not differ from the other physiognomies concerning plant species richness, although it had more, thinner and shorter plants. Among primary sites, there was an uphill gradient of increasing density and crown height and decreasing total height and basal area of individual plants. From the four physiognomies, HT had the highest bird species richness, although BV was the more structured forest site. Plant height, specific fruiting plants and a high spatial heterogeneity may be resulting in such a high diversity in HT. Concerning bird guilds, understory insectivorous birds preferred SF, what may be related to the high density of the understory and thus a high availability of foraging microhabitats. Some generalist frugivores followed this same pattern, while others preferred sites with a high abundance of specific plants, as Rubiaceae, and no frugivore guild preferred sites with the highest total abundance of fruits. Seedeaters, represented by one species, preferred one specific sample unity of one site where their main food item was fruiting. Nectarivores and canopy insectivores did not seem to be related to any of the variables studied. Thus, plant habits, vegetation structure and plant composition variables influenced habitat selection by birds, but the degree of importance of each variable varied among guilds. Also, neither vegetation structure nor plant richness alone determined understory bird species richness.

Key words: bird, community, guild, species richness, spatial pattern, physiognomy, vegetation structure, habitat selection, phenology, Atlantic Forest, tropical forest, Brazil.

INTRODUCTION

Distributions of birds are more accurately known than those of any other group of organisms. However, much remains to be learned what limits bird distribution (Greenwood 1992). An association between increasing structural complexity of the habitat, for example, along some environmental gradient, and increasing bird species diversity has been demonstrated in many studies, both in and out of the tropics (Karr and Roth 1971, Terborgh 1977, Hino 1985, Allegrini 1997, Goerck 1999). The consistency of this result, as well as the ability to predict the presence or absence of particular bird species from structural measurements (specially the vegetation structure) of the habitat (MacArthur *et al.*1962), has led to a widespread conviction that the structural qualities of a habitat are paramount in determining its occupancy by birds.

However, the relationship between vegetation structure and bird community sometimes is hard to identify and can be affected by physical differences or historical factors or a combination of both (Pearson 1975, Fleming *et al.* 1987). Sometimes the relationship can exist in tandem with microclimatic conditions acting on physiological limitation in birds (heat and water balance) and/or on the availability of food resources (Karr and Freemark 1983).

In some cases, plant species composition has been shown to be a more important predictor of bird community structure than vegetation structure. In this way, researchers have demonstrated the fidelity of some birds to a particular plant species (Rotenberry 1985). This can happen due to the scale of observation employed by the investigator (Wiens 1989). If one compares woods of very different structures (in terms of, for instance, their foliage profiles) or at very different successional stages, then the structure appears to be more important. If similar in these respects, then the plant composition may emerge as a strong influence (Wiens and Rotenberry 1981, Greenwood 1992). However, MacNally (1990 *apud* MacNally 1995) showed that both, vegetation structure and floristic composition might influence bird communities. For example, some species select habitats for structural reasons, while others for the floristic composition and still others for both reasons.

Most studies have examined structural or floristic components of vegetation with bird community separately. However, given that both factors may not operate to influence bird communities, it is not sufficient to examine only one component. Here we examine simultaneously important characters of the habitat, such as plant composition, plant habits, vegetation structure and plant phenology, to understand which characteristics best explain patterns of bird abundance and species richness.

The Atlantic Forest is an excellent system for this kind of investigation because it is formed by a mosaic of vegetation types of primary forests and forests with successional differences (natural and human disturbance). Besides this, the Atlantic Forest is considered one of the hotspots of bird species diversity, with many species endemic or threatened and with restricted distribution (Parker *et al.* 1996, Meyers *et al.* 2000). Many studies have attributed this high diversity of species to the altitudinal variation (Parker *et al.* 1996, Goerck 1999). However, the physiognomic variation also likely contributes to explaining high avian diversity. Mantovani *et al.* (1990) described different physiognomies in primary forest in Atlantic Forest. These physiognomic variations are mainly correlated with the soil type and not only the elevation. In this paper, we compared the composition and structure of bird community in different types of vegetation by asking the following questions:

(1) How do bird communities differ in species composition, richness and number of bird captured among four habitat types (*i.e.*, hilltop, middle slope and bottom of valley in primary forest and one in secondary forest)?

(2) Do different ecological groups of the community (guild) differ in their sensitivity to variation on vegetation structure, plant composition and resource abundance among habitats? Which of these factors most affect capture rates of birds?

(3) Is the variation among habitats stronger than within habitat in relation to the vegetation structure and bird community?

MATERIAL AND METHODS

STUDY AREA

The study was conducted in four Atlantic Rain Forest sites in the Parque Estadual Intervales (PEI) in southern São Paulo State, southeastern Brazil (Fig. 1. 1). The average annual rainfall is 1,500 to 1,800 mm and temperature is 17 to 19°C (SMA 2001). PEI is a 49,000 ha protected area surrounded by three other reserves encompassing a total of 120,000 ha of continuous forest. PEI is composed of different types of forest physiognomies along an altitudinal gradient ranging from 60 to 1,100 m a.s.l., with climate and soil also varying along this gradient (Mantovani 2001). PEI also has patches of second growth vegetation due to past human disturbance. These areas were formerly occupied by plantations, pastures and logged forests and abandoned in 1985 when the park was established. The vegetation in these physiognomies is classified as Lower Montane Rain Forest (700-1,100 m), and is considered to be "typical" Atlantic Forest (Oliveira-Filho & Fontes 2000). The hilltop (HT) is located at "Mirante da Anta" (24°16' 42''S and 48° 24' 28''W) at *ca* 1,000 m elevation. Due to variations in the soil depth, hilltop forest can also differ in vegetation structure, varying from a transitional type with middle slope forest to an altitudinal shrubs or even species typical of secondary forest. The middle slope (MS) is located at "Barra Grande" (24°18' 17''S and 48° 21' 53''W) at about 900 m elevation. The canopy is 15-20 m high. The bottom of valley (BV) is located at "Carmo" (24°18' 60''S and 48° 25' 00''W) at about 700 m elevation. The irregular canopy is 20 m high with emergent individuals up to 30 m. The secondary forest (SF) is located at "Sede" (24°16'09" S 48°24'56" W) at about 800 m elevation in the middle slope (see Gomes and Silva 2003). Sede was an area cowered mainly by plantations 50 years ago and since 1985 has been abandoned and undergoing natural regeneration. For a detailed description of vegetation at PEI see Mantovani *et al.* (1990).

We selected the localization of four study sites by vegetation type and topographic zone, three of them in primary forest and one in secondary forest, to cover the existing environmental variation. The primary forest sites included hilltop, middle slope and bottom of valley (Mantovani *et al.* 1990). In each primary forest site five sample units were established for local vegetation sampling, phenological data and as sites for mist nets. Nearest neighbor distance among the units of the same habitat varied from 10 m to 1,000 m and from 2,000 m to 10,000m between habitats. Because much of the study areas were too rugged to accommodate the mist nets, we were forced to choose sites based on an additional feasibility criterion. These units were determined a priori to produce an independent data set from each habitat type for statistical analyses.

BIRD COMMUNITY

Although mist nests are known to introduce bias in estimates of bird community structure and dynamics (specially for canopy and less active species), we use this method because it provide identical sampling of different habitat and its accuracy is relatively independent of observer biases and skills (Levey 1988, Blake and Loiselle 2000, Pearman 2002).

Birds in each primary forest habitat five units were sampled with 10 mist nets per unit (36 mm mesh, 12 x 2.5 m). We placed the nets in line on these units and each unit were sampled one day each month during one year (total sampled BV+MS+HT=10,800 mist-net-hours). They were open from dawn to early afternoon (6 hours). We checked nets at least once per hour and more frequently during rain. Due to the more restricted area in secondary forest we reduced to six the number of nets per unit (total sampled in SF 2,160 mist-net-hours). The MS and SF were sampled from April 1999 to March 2000, BV from April 2000 to March 2001 and HT from April 2001 to March 2002.

All the birds were identified following Dunning (1989), Frisch (1981) and Sick (1997). After this, they were banded with numbered aluminum leg bands, with exception to the Trochilidae. Species captured were assigned to distinct ecological groups (guild) based on feeding habitats, foraging substrate, and preferred foraging strata in the vegetation. This classification was based on Willis (1979), Allegrini (1997) and Aleixo (1999) into: diurnal carnivores (DC), large canopy frugivores (C-LF), edge frugivores/insectivores (E-FI), canopy frugivores/insectivores (C-FI), understory frugivores/insectivores (U-FI), edge seedeaters (E-S), terrestrial seedeaters (T-S), bamboo insectivores (BB-I), canopy insectivores (C-I), nocturnal insectivores (No-I), understory insectivores (U-I), terrestrial insectivores (T-I), trunk and twig insectivores (TT-I), nectarivores/insectivores (NI), edge omnivores/insectivores (E-OI) (Appendix 1.1). Canopy species were included in the analyses because the units were topographically rugged and, sometimes, nets could sample the canopy. Besides this, most of birds typical of the canopy are not restricted to the canopy, they can be seen sometimes in the understory in function of the variation on resource availability among the vertical stratification (Levey 1998, Loiselle and Blake 1991). Although diurnal carnivores (DC) and nocturnal insectivores (No-I) were sampled, we excluded these guilds in the CCA (Canonical Correspondence Analysis) and linear regression analyses because of the reduced number of captures.

ENVIRONMENTAL DATA

Several variables were evaluated at each habitat to provide a quantitative characterization of forests for use in CCA ordination and linear regression analyses. We expected bird community structure to vary with vegetation structure, plant composition and food availability at the habitats, so we used several measures describing variation in these characteristics.

Vegetation structure – Within primary forest units we established three plots of 10 x 25m distributed along the line of mist nets and distant 1m of the line. Each plot was subdivided into 25 subplots of 10 m^2 (1 x 10 m), from which eight subplots were randomly selected for sampling (1,200 m^2 - total area sampled in each habitat). In each subplot we collected the following information for all the plants higher than 1.3 m: total height (TH), bole height (BH), canopy depth (TH-BH), diameter at breast height (dbh) and plant habit (shrub, tree, bamboo, liana, herb, dead plant, palm or fern). Within secondary forest units we used the same methods but reduced in two the number plots for each unit (800 m^2 total area sampled) due to the more restricted area in relation to the others habitats.

Plant composition – For characterization of plant composition in each habitat, we sampled in the plots only the zoochorous plants that produce fleshy fruits, because they clearly correlated with frugivorous birds and influence their habitat selection (Loiselle and Blake 1991).

Phenological data - All the plots were monitored monthly during one year at the same time that birds were captured. The fruiting plants were counted, identified and individually marked. We used three phenological variables: number of fruiting plants, number of fruiting plants species and fruit abundance. The fruit abundance was classified based on what was proposed for tropical forests by Levey (1988). According to this method, we indexed ripe fruit abundance for each plant on a scale of 1-8 (1 = 1 – 10 ripe fruits, 2 = 11 – 25, 3 = 26 – 50, 4 = 51 – 100, 5 = 101 – 200, 6 = 201 – 500, 7 = 501 – 1000, 8 >1001). We judged ripeness based on changes in fruit color and softness during maturation.

STATISTICAL ANALYSIS

Environmental characterization and comparison among habitats - We compared the habitats in relation to fruiting plant species composition, diversity and richness using the similarity index of Sorensen (Magurran 1988) and the rarefaction method (Krebs 1999). We calculated rarefaction curve using a Monte Carlo simulation procedure (Ecosim 7.0; Gotelli and Entsminger 2001) that also allows a comparison of number of species expected per habitat based on the lowest number of individuals recorded among the habitats compared; that is, species richness is compared based on the same number of individuals. Simulations were run 100 times and mean expected number of species at each habitat were compared based on the 95% CI.

Due to differences in samples effort between the primary and secondary habitats, some vegetation structure variables (total height, bole height, depth canopy, plant basal area) were compared by the median of individual sampled in each unit. The plant habits (tree, shrub, liana, herb, dead plant, fern, palm and bamboo) were analyzed by the total number of individuals in each unit per m^2. The phenological data (number of fruiting plants, number of fruiting plant species and the fruit abundance index) were compared by the median of number of fruiting plants on 12 months in each unit. We compared the habitats using multivariate analysis of variance (MANOVA) and Tukey HSD test for the significant variations to verify which variables affect the variation and what habitats are different from each other (Finch 1989).

Comparison of bird communities – Bird communities were compared among habitats using the similarity index of Sorensen (Magurran 1988) and the rarefaction method (Krebs 1999). Similarly to plants, to account for differences in bird sample effort we used the average of birds captured within guilds at each habitat. We applied the Anova and Tukey HSD test to verify the difference between habitats.

Evaluating the influence of vegetation structure, plant composition and resource abundance on the number of birds captured within guilds - We used the canonical correspondence analysis (CCA) to describe the relationship between the number of capture within guilds and the vegetation and phenological variables. CCA is an ordination technique that incorporates multiple regressions, with the ordination axes constrained as linear combinations of environmental variables. CCA also allows a statistical significance test on the correlations between species abundance and environmental variables supplied, which is Monte Carlo permutation test (Ter Braak 1986). Before applying this analysis, we submitted the variables to principal components analysis (PCA) to produce a smaller set of synthetic variables (Pearman 2002). We did three PCA, one for vegetation structure, another for plant habits and other for phenological data. Matrix of vegetation structure consisted of six variables (density of individuals, total basal area, median of plant basal area, median of bole, median of height and median of canopy depth) for each unit, the plant habit matrix had eight variables (density of shrub, tree, bamboo, liana, herb, dead plant, palm and fern) and phenological data three (median of number of fruiting plants per m^2, median of number of fruiting plants species per m^2 and median of index of fruit abundance per m^2). Following the PCA results, we used the factor 1 of these PCA (structure 1, plant habit 1 and phenology 1) and other 6 variables (total basal area, density of bamboo, density of Lauraceae, Melastomataceae, Myrtaceae and Rubiaceae) selected by their relevance on PCA and their biological interest as descriptors of habitat variations in the Canonical Correspondence Analysis (CCA). By applying this analysis, we organized the data of guilds and vegetation variables in two distinct matrices, as required by CCA. The guild matrix consisted of the number of bird captures per mist-net-hour within guilds for each unit. No-I and DC were excluded of the matrix because they had small number of captures. The other matrix consisted of the nine vegetation variables (structure 1, plant habit 1, phenology 1, total basal area, density of bamboo, density of Lauraceae, Melastomataceae, Myrtaceae and Rubiaceae) for each unit. We used the CCA to describe overall patterns in the guilds data set, not to measure the contribution of each variable and verify its statistical significance. For this measurement, we applied the multiple linear regression analysis for vegetation structure, plant habits and phenological variables to examine which of these variables could exert a stronger influence on bird capture.

Differences inter and intra-habitats – We compared the variation inter and intra-habitats in relation of bird communities and vegetation structure and plant composition using CCA. The more close the unit points of one habitat along the CCA ordination axes, the more homogeneous is the habitat. The position where the unit tended to occur along the gradients in the environmental variation space indicates which variables are more affecting this variation.

All these statistical analysis were performed procedures using Statistica Program (1993) and PC-ORD 4.10 (Mc Cune and Mefford 1999).

RESULTS

1. Characterization of habitat types

Plants composition and species richness - We recorded 101 species of fruiting plants from 31 families (603 individuals). Rarefaction curves indicated that new species still were being recorded at all habitats (i.e. no indication of asymptote, Fig. 1. 2), mainly in BV, where the rate of new species added was high. At the same number of fruiting plants (n=81), BV and MS showed significantly higher richness than HT and did not differ from each other. SF was not significantly different from the other three habitats (Table 1. 1, Fig. 1. 2).

Plant species composition differed among the physiognomies and only *Mollinedia floribunda* (Monimiaceae) was present in all habitats. The highest similarity occurred between BV and MS, while the lowest was between SF and HT (Table 1. 2).

Vegetation structure and plant habit – The habitats showed significant difference in relation of the vegetation structure and plant habit (Table 1. 3). All the structure and plant habit variables contributed for these general differences, with the exception of total basal area, density of fern and density of bamboo (Table 1. 4). SF had the highest density of individuals on the understory, mainly in function of the high density of shrubs and herbs (Table 1. 5). SF showed similarity with HT in several vegetation variables, like median of bole height, median of total plant height, median of plant basal area, density of tree and density of dead plants (Table 1. 4). Among the primary forests most variables presented a gradual variation from BV to HT. According to Table 1. 4 and 1. 5, the variation seems to exist but it is increase variation to HT in plant density, canopy depth and trees. In bole, height, individual basal area, shrub, liana, herb and palm it is decrease variation to the same direction and in dead plant it apparently has no definite direction.

Phenological data – The habitats differed significantly on phenological data (Table 1. 3). The main variables that contributed for this difference were the number of fruiting plants and fruiting species where MS showed the smallest values (Table 1. 4 and 1. 5).

2. Bird community variation among habitats

A total of 2280 captures (12,960 net-hours) of 117 species from 24 families were recorded in all four physiognomies (Appendix 1. 1). Species accumulation curves indicate that new species still were being recorded at all habitats, but that the rate at which new species were being added in HT was higher than in the other areas (Fig. 1. 3). Species richness based on capture data was significantly higher in HT than in the other physiognomies at the same number of bird captured (*e.g.* n=350) (Table 1. 6 and Fig. 1. 3). Other habitats did not differ from each other. The lower number of captures in HT suggests that species captured in HT were represented by few individuals.

Bird species composition differed among the habitats, although similarity was higher than among fruiting plants (23 species were captured in all the habitats) (Table 1. 7). BV and MS were the most similar areas in bird species richness, while HT and SF were the less similar ones. The same pattern was found for plants (see above).

Captures rates within guilds differed among habitats but only five guilds differed significantly among habitats (Fig. 1. 4 Anova, $p<0,05$; Tukey, $p<0,05$). Understory insectivores (U-I), terrestrial insectivores (T-I) and edge omnivores/insectivores (E-OI) were captured more frequent in SF. MS had more captures of edge seedeaters (E-S) and BV and SF of understory frugivores/insectivores (U-FI.)

3. Effect of habitat variation on capture rates of birds within guilds

Preliminary analyses for vegetation variables reduction –In order to produce a smaller set of synthetic variables for vegetation variables of the habitats, we constructed four PCA that summarized different aspects of vegetation: vegetation structure, plant habits, plant species composition and phenological data.

a) Vegetation structure – The factors 1 and 2 of PCA accounted for 83.0% of the total variance (Appendix 1. 2a). The first principal component (structure 1) extracted 63.1% and the second principal component extract an additional 19.9% of the variance. Inspection of the eigenvectors indicated that median of plant basal area; median of bole height and median of plant height dominated the first PCA axis and were negatively correlated to this axis. The second axis was more influenced by the total plant basal area, also negatively correlated to it. However, total basal area was not strongly represented in any axis and was considered important to describe habitat. Then, it was picked up as another variable to enter in CCA analysis.

b) Plant habits – The first three factors of PCA accounted for 71.4% of the total variance (Appendix 1. 2b). Contributing most to the first principal component (plant habit 1) (34.3%) were number of shrubs/m^2, number of herbs/m^2 (both positively correlated) and number of palms/m^2 (negatively correlated). The second axis (22.1%) was mainly influenced by number of lianas/m^2 and the third axis (15.0%) by number of ferns/m^2 and number of bamboos/m^2. Number of bamboos/m^2 was not well represented in the first axis and was considered important to describe habitat. Then, it was picked up as another variable to enter in CCA analysis.

c) Phenological data – The first two factors of PCA accounted for 94.5% of the total variance, and the first principal component (phenology 1) (75.2%) was influenced positively by median of number of fruiting plant species, median of number of fruiting plants and median of fruit abundance index (Appendix 1. 2c).

d) Plant composition – A PCA could not represent well most of the plant families abundances. Then, density of Lauraceae, Melastomataceae, Myrtaceae and Rubiaceae were chosen to enter the CCA due to their importance to frugivorous birds, as reported by many authors (Wheelwright *et al.* 1984, Snow 1981, Loiselle and Blake 1990, Pizo 2002).

Bird community correlations with synthetic vegetation variables –The first three axes of canonical correspondence analysis (CCA) had a total 0.45 of inertia and explain 58.9% of the total variance. The structure 1 and plant habit 1 were both associated with negative scores on the first ordination axis and Rubiaceae and Melastomataceae with the positive scores. The first ordination axis was significant (Monte Carlo permutation test, 100 runs, p= 0.01; Appendix 1. 3) and explained 32.5% of the variation in the species occurrence data. The second canonical axis was primarily associated positively with the variation in the number of individuals of Rubiaceae with number of ripe fruits/m^2

and negatively with the number of bamboos/m^2. This axis was marginally significant (Monte Carlo permutation test, 100 runs, p= 0.08) and explained 20.6% of the data variation.

Examination of the sample units' scores along the CCA axes indicated that structure 1 and plant habit 1 strongly influenced the separation of the secondary forest units from primary forest units (Fig. 1. 5). The SF units were more similar in terms of vegetation variables and bird captured than the primary forest units, as seen by the broad dispersion of the unit points on CCA axes (Fig. 1. 5). The separation of primary forest units was mainly determined by the variation on the abundance of Rubiaceae, plant habit 1 and number of bamboo, that were related with the second axis. The primary forest units were distributed on a gradient along this axis. BV units were distributed near the origin of the CCA and were defined by the intermediate characterization in relation to the other habitats. MS and HT were more heterogeneous and have units (MS3 and HT2) with particular habitat specialization with high density of bamboo in MS3 and abundance of Rubiaceae in HT2.

In relation of capture rates within guilds, the CCA axes showed that the high availability of fruit of Rubiaceae in HT2 was correlated with high number of frugivorous birds captured (canopy frugivore/insectivores C-FI, edge frugivores/insectivores E-FI and large canopy frugivores LC-F) (Fig. 1. 5). The same happened with the fructification of the bamboo in MS3 that was correlated with the high capture of edge seedeaters (E-S), *Haplospiza unicolor,* which could not be shown by CCA, as it was not directly related to density of bamboos.

Capture rates of edge omnivores/insectivores (E-OI), terrestrial insectivores (T-I), understory insectivores (U-I), terrestrial seedeaters (T-S) were higher in SF units that were positively influenced by the structure 1 and plant habit 1. The correlation with these variables showed that these guilds were closely correlated with the high density of thin individuals on understory (mainly shrubs and herbs) (Appendix 1. 2a and 1. 2b). Bamboo insectivores (BB-I), trunk and twig insectivores (TT-I), understory frugivores/insectivores (U-FI), canopy insectivores (C-I) and nectarivores/insectivores (N-I) were positioned on the multidimensional space on the CCA axes near the origin of ordination space. Then, the variables studied did not seem to have influenced, or influenced very little, capture of these five guilds.

Evaluation of the specific correlations between vegetation variables and guilds - The multiple linear regression between all the vegetation structure, plant habit and phenological variables and the capture rates with guilds indicated that the plant habits variables had more significant relation with the guilds than any other vegetation variables of the habitats. The plant habits had seven significant relations, the structural variables had four and the phenological data just one. Variations on degree of importance of variables among guilds showed that guilds responded to habitat variations idiosyncratically. The preferential conditions to increase the number of bird captured were different for each guild.

a) **Plant habit** – Guilds that had significant relations were E-FI, C-FI, U-FI, E-OI, BB-I, T-I and TT-I. The principal variables that most influenced these relations varied among the guilds, but two variables probably were stronger than the others: density of herbs, for the insectivores guilds (BB-I, U-I and TT-I) and density of dead plants for the frugivores guilds (E-FI, C-FI, U-FI and E-OI) (Table 1. 8).

b) **Structural variables of the vegetation** – Guilds that had relations were E-OI, BB-I, U-I and T-I. The importance of the structural variables varied among the guilds, but there were more intense relations with the insectivore guilds (Table 1. 9).

c) **Phenological data** - Only T-I had a slight relation with the phenological data. The variables that were mainly correlated were number of fruiting plants and number of fruiting plant species (Table 1. 10).

4. **Differences on inter and intra-physiognomic variation** – According to the CCA ordination there was a clear difference between secondary forest and primary forest units in relation to vegetation variables and the capture rates within guilds (Fig. 1. 5). SF units differed mainly on vegetation structure and plant habits and showed less intra-physionomic variation than primary forest units. Among the primary forest units, the plant species composition mainly divided the units but there was not a clear distinction among the physiognomies because of the high intra-physiognomic variation.

DISCUSSION

1. Vegetation variations on physiognomies

Although the difference in species richness is not expressive, physiognomies differ strongly in plant species composition. According to Burns and Leathwitck (1996 *apud* Webb *et al.* 1999), differences on topography, soil structure, streams and light exposition, can affect the spatial distribution of plant species because they influence the seedling survival and then can be a criterion of species selection.

Structurally, the primary forest physiognomies showed an increase gradient from BV to HT of higher density of thin and short plants. Many factors interrelated, like soil type, soil depth, and climatic conditions can affect the vegetation structure (Webb *et al.* 1999). Although these data were not measured in this study, Mantovani (2001) showed that the hilltop at PEI have shallow soil with a small nutritional retention. Besides this, the organic decomposition in the soil is slower by low temperatures and less moisture. These conditions usually lead a forest with high density of thin and short individuals. On the other hand, the soils at bottom of valley, are deeper and experience a more stable microclimatic condition, allowing the development of a forest with high complexity and diversity, in which some individuals can reach 25 to 30m.

Although SF showed a high value of species richness compared to the primary forest sites (Table 1. 1), the vegetation structure, mainly influenced by a high density of thin individuals on the understory (trees, shrubs and herbs), still separated this physiognomy from thee other ones. With regard to the within variation of the habitats, SF was smoother than other physiognomies. Two factors may be contributing to a relatively low spatial heterogeneity on the occurrence of numerous thin individuals: the age of this forest site (considering the beginning of the secondary succession as age zero) and the more restricted area sampled (a lower spatial heterogeneity may have been sampled).

The steep relief associated with heavy rainfall and stormy can explain this high heterogeneity within the primary forest physiognomies. In these situations landslides are frequent, which directly affect the plant population dynamics and promotes spatial heterogeneity with patches of forests in different successional stages on the landscape (Mantovani 2001). Another factors that shows the instability of primary forest habitats is the high density of bamboo, since these aggressive plants quickly invade and colonize recently formed gaps (Tabarelli and Mantovani 2000).

2. Effect of physiognomic variation on bird communities

2.a. Species richness and composition

The bird communities were sensitive to the variation in floristic and vegetation structure among physiognomies and showed particular preference for some specific positions along a gradient of environmental conditions with different groups or guilds being differentially tolerant to variations in these conditions (Kirk *et al.* 1996). This association between birds and habitat components can reflect a direct dependence on survival (e.g. nestling, physiology, predation risk) or indirectly by the dependence on their preys or fruiting plants, which can vary temporally (Cody 1981, Thiollay 1999b). A more tight dependence on these variables cause some species (e.g. *Anabacerthia amaurotis, Basileuterus rivularis, Lipaugus lanioides, Stephanophorus diadematus* and *Ramphodon* *naevius*) to be infrequently observed and patchily distributed among habitats (Terborgh *et al.* 1990). On the other hand, species more tolerant to the variation pattern of vegetation structure may occur in all habitats, although with some differences in abundance (e.g. *Haplospiza unicolor, Mionectes rufiventris, Trichothraupis melanops*). For mobile species that usually track the variation in food availability among different habitats (Chapter 3), the movements into or out habitats during food scarcity (Levey 1988) could increase the similarity of bird species among habitats (Dyrcz 1990).

Human disturbances on forest habitats can reduce species richness and alter species composition according to the disturbance degree (Ding *et al.* 1997). In the present study, differences on species composition were more evident than richness, comparing primary and secondary units. In the SF units the absence C-LF captures was probably because species of this guild are usually more sensitive and prone to local extinction, sparsely or patchily distributed, or very specialized and intolerant to the second growth vegetation surrounding fragments (Turner 1996, Goerck 1999). Its is very plausible that anthropogenic disturbance could reduce the abundance of some plant species what were important as a resource by this guild and consequently, it had led to an impoverished of this group in the community (Tabarelli *et al.* 1999). Additionally, the disturbance favored the immigration and colonization of generalist species (e.g. *Saltator similis*) and/or increase their abundance, as seems to be the case with the guild of E-OI (e.g. *Tachyphonus coronatus, Basileuterus culicivorus*) (Aleixo 1999).

The expected pattern of high structurally complex vegetation leading to an increase in the bird species richness and diversity (Willson 1974, Finch 1989, Goerck 1999), was not found in BV, but in HT. The explanation for this result may be attributed to the following reasons:

(1) Method limitation in bird sampling - the use of mist nets certainly excluded many large canopy species on BV, MS and SF, where the canopy was high (Blake and Loiselle 2000). This same method, however was effective in capturing canopy species in HT, with a short canopy (Blake

and Loiselle, unpublished data). This potential bias does not explain, however, the expressive high capture of frugivorous species and the low capture of insectivorous and seedeater birds;

(2) Association among frugivorous birds and fruiting plants – The high abundance of some fruit plants (*Psychotria vellosiana, Miconia budlejoides, Gomidesia affins,* and *Myrsine gardneriana*) in HT could increase species richness of C-FI, E-FI and LC-F (Loiselle and Blake 1993), probably exerting a stronger impact on specialized frugivores (Rotenberry 1985);

(3) Local high spatial heterogeneity – The vegetational types at hilltop included patches of middle slope forest, altitudinal shrub or species typical of secondary forest, a pattern frequently found in the Atlantic Forest (Mantovani 2001). This local spatial heterogeneity could eventually increase the local bird species richness (Karr and Roth 1971, Thiollay 1999a, Webb *et al.* 1999).

2.b. Guild variations among physiognomies

The understory insectivores' guilds preferred mainly the SF units, which were characterized by a high density of thin individuals of shrub, herb and dead plants. Karr and Freemark (1983) also found significant differences in the activity patterns of birds with shrub density variation. In addition, Garcia *et al.* (1998) have shown that bird abundance was being influenced by density of plants, total height, basal diameter and number of vertical layers. Probably, the architectural structure of the vegetation in secondary forests (e.g. foliar arrangements, position and accessibility of available substrates, high structural diversity) may favor a high availability of food resources because arthropods may have preference for certain plant species and/or physical attributes of the substrates (Cody 1981, Robinson and Holmes 1982, Terborgh 1985, Holmes and Recher 1986). In the primary forests habitats, the capture of insectivorous birds decreased towards hilltop and were more closely related to the structural and plant habit variables of the habitats. Both direct (e.g. physiological bird limitation) and indirect (e.g. physiological prey limitation) effects of these variables could be operating to determine this pattern of bird distribution along the altitudinal gradient (Sabo 1980, Pearman 2002). Concerning the indirect effect, the ant-following birds may choose areas where ants are active and army ants are particularly sensitive to low humidity and high temperatures (Schneirla *et al.* 1954 *apud* Pearman 2002) conditions found in HT that could decrease ants and, as a consequence, ant-followers.

The high abundance of E-S (*Haplospiza unicolor*) on MS probably was an unusual event associated with the bamboo sporadic flowering, which occurred during this study. According to Olmos (1996) *Haplospiza unicolor* has its breeding cycle closely related to the flowering of one bamboo species (*Chusquea aff. meyeriana*). Goerck (1999) also explained that *Haplospiza unicolor* is a endemic bird specie in Atlantic Forest with a specialist forager on bamboo seeds. Our data indicate that the fluctuation observed in the *Haplospiza* abundance resulted from movements into and out of the habitats following the patchy distribution of bamboo species as well as their unpredictable fruiting pattern (Pearson *et al.* 1994).

Nectarivores showed no significant difference among the habitats and no relationship with the vegetation structure, plant composition, plant habit or phenological data. The same pattern was found by Pearman (2002). This results suggest that other factors not considered here might be more determinant on the distribution of nectarivores, like altitudinal variation associated to a particular plant species not sampled in these habitats (Buzato *et al.* 2000), abundance of flowers (Blake and Loiselle 2001), or other flower traits (*e.g.* sugar content in the nectar, corolla length) (Terborgh 1985).

Among the frugivores we found two different patterns: (1) E-OI and U-FI differed between the habitats and were more correlated to the vegetation structure and plant habit, being more abundant on where the understory was more dense. The bird interest on SF understory was probably due to the high abundance of bird fruiting plants (e.g. Nyctaginaceae, Piperaceae, Musaceae and Commelinaceae) and because it offered additional resources or needs (e. g. insect prey, nesting areas, etc.) (Cody 1981); (2) C-FI, E-FI and C-LF, although presenting no significant differences between physiognomies, were more correlated to the abundance of Rubiaceae, Myrtaceae and Melastomataceae in spite of the total abundance of fruits. The lack of a relationship between bird abundance and phenological data among the frugivorous guilds suggests that the availability of fruits is not a major factor limiting the bird abundance and distribution. The local high fruit availability in all physiognomies (Jordano 1987) and the flexibility on feeding items of some bird species may result in a weak response of frugivores to spatial variation on fruit availability.

3. Floristics or physiognomic criteria for habitat selection in birds?

Our data support the idea of Mac Nally (1995) of a relation between bird community's spatial variation and habitat selection. Ultimately, habitat selection in birds is the corollary of the interaction between several vegetation variables, although the degree of importance of each one varies among different bird guilds. Vegetation structure and plant plant habit seem to have a stronger influence on insectivores and some frugivores/insectivores, while plant composition plays a more important role for other frugivores and probably for seed-eaters.

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LITERATURE CITED

ALEIXO, A. 1999. Effects of selective logging on a bird community in the Brazilian Atlantic forest. *Condor* 101(3): 537-548.

ALLEGRINI, M. F. 1997. *Avifauna como possível indicador biológico dos estádios de regeneração da Mata Atlântica*. Tese (Mestrado). USP. 161 p.

BLAKE, J. G., and LOISELLE, B. A. 2000. Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. *Auk* 117 (3): 663-686.

BLAKE, J. G., and LOISELLE, B. A. 2001. Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. *Auk* 188(2): 304-326.

BUZATO. S., SAZIMA, M., and SAZIMA, I. 2000. Hummingbird-pollinated floras at three Atlantic forest sites. *Biotropica* 32(4b): 824-841.

CODY, M. L. 1981. Habitat selection in birds: The roles of vegetation structure, competitors and productivity. *BioScience* 31: 107-113.

DING, T-S., LEE P-F., and LIN Y-S. 1997. Abundance and distribution of birds in four, high elevation plant communities in Yushan National Park, Taiwan. *Acta Zoologica Taiwanica* 8(1): 55-64.

DUNNING, J. S. 1989. *South American Birds. A photographic aid to identification*. Harrowood Books, Newton Square. 315p.

DYRCZ, A. 1990. Understory bird assemblages in various types of lowland tropical forest in Tambopata Reserve, SE Peru (with faunistic notes). *Acta Zool. Cracov*. 33(11): 215-233.

FINCH, D. M. 1989. Habitat use and habitat overlap of riparian birds in three elevational zones. *Ecology* 70(4): 866-880.

FLEMING, T. H., BREITWISCH, R., and WHITESIDES, G. H. 1987. Patterns of tropical vertebrate frugivore diversity. *Ann. Rev. Ecol. Syst.* 18: 91-109.

FRISCH, J. D. 1981. *Aves brasileiras.* Vol. I. Dalgas-Ecoltec Ecologia Técnica e Comércio Ltda, São Paulo. 353p.

GARCIA, S., FINCH, D. M., and LEON, G. C. 1998. Patterns of forest use and endemism in resident bird communities of north-central Michocan, Mexico. *Forest Ecology and Management 110*: 151-171.

GÖERCK, J. M. 1999. Distribution of birds along an elevational gradient in the Atlantic forest of Brazil: Implications for the conservation of endemic and endangered species. *Bird Conservation International* 9(3): 235-253.

GOMES, V. S. M., and SILVA, W. R. 2003. Spatial variation in understory frugivorous birds in an Atlantic Forest fragment of southeastern Brazil. *Ararajuba* 10(2): 219-225.

GOTELLI, N. J., and ENTSMINGER, G. L. 2001. *EcoSim: Null models software for ecology.* Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsmin/ecosim.htm.

GREENWOOD, J. J. .D. 1992. Understanding bird distributions. *Tree* 7(8): 252-253.

HINO, T. 1985. Relationships between bird community and habitat structure in shelterbelts of Hokkaido Japan. *Oecologia* 65(3): 442-448.

HOLMES, R. T., and RECHER, H. F. 1986. Determinants of guild structure in forest bird communities an intercontinental comparison. *Condor* 88(4): 427-439.

JORDANO, P. 1987. Avian fruit removal: effects of fruit variation, crop size, and insect damage. *Ecology* 68:1711-1723.

KARR, J. R., and FREEMARK, K. E. 1983. Habitat selection and environmental gradients: Dynamics in the " stable" tropics. *Ecology* 64(6): 1481-1494.

KARR, J. R., and ROTH, R. R. 1971. Vegetation structure and avian diversity in several new world areas. *American Naturalist* 105(945): 423-435.

KIKKAWA, J. 1983. Ecological association of birds and vegetation structure in wet tropical forests of Australia. *Australian Journal of Ecology* 7(4): 325-346.

KIRK, D. A., DIAMOND, A. W., HOBSON, K. A. and SMITH, A. R. 1996. Breeding bird communities of the western and northern Canadian boreal forest: relationship to forest type. *Can. J. Zool.* 74: 1749-1770.

KREBS, C. J. 1999. *Ecological Methodology* 2 ed. Addison –Wesley Educational Publishers Inc. p.620.

LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58(4): 251-269.

LOISELLE, B. A. and BLAKE, J. G. 1990. Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. *Studies in Avian Biology 13*: 91-103.

LOISELLE, B. A. and BLAKE, J. G. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72(1): 180-193.

LOISELLE, B. A. and BLAKE, J. G. 1993. Spatial distribution of understory fruit-eating birds and fruiting plants in a neotropical lowland wet forest. *Vegetatio* 107/108: 177-189.

Mac NALLY, R. C. 1995. *Ecological versatility and community ecology.* Cambridge University Press. 435 p.

MacARTHUR, R. H., MacARTHUR, J. W., and PREER, J. 1962. On bird species diversity II. Prediction on bird censuses from habitat measurements. *American Naturalist* 96:167-174.

MAGURRAN, A. E. 1988. *Ecological diversity and its measurement.* Croom Helm, London. 179p

MANTOVANI, W. 2001 *A paisagem dinâmica.* Pp. 81-91. *In:* Leonel, C. Intervales. Fundação para a conservação e produção florestal do Estado de São Paulo. Secretaria de Estado do Meio Ambiente.

MANTOVANI, W., RODRIGUES, R. R., ROSSI, L., ROMANIUC-NETO, S., CATHARINO, E. L. M. and CORDEIRO, I. 1990 *A vegetação na Serra do Mar em Salesópolis, SP.* Pp. 1: 348-384. *In*: II Simpósio de Ecossistemas da Costa Sul e Sudeste Brasileira: estrutura, função e manejo, Academia de Ciências do Estado de São Paulo, Águas de Lindóia.

McCUNE, B. and MEFFORD, M. J. 1999. *PC-ORD for Windows. Multivariate analysis of ecological data.* version 4.10. MjM Software, Gleneden Beach, Oregon, USA.

MEYERS, N., MITTERMEYER, R. A., MITTERMEYER C. G., FONSECA G. A. B., and KENT J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.

OLIVEIRA –FILHO, A. T., FONTES, and M. A. L. 2000. Patterns of floristic differentiation among Atlantic Forests in Southeastern Brazil and the influence of climate. *Biotropica* 32(4b):793-810

OLMOS, F. 1996. Satiation or deception?: Mast-seeding *Chusquea* bamboos, birds and rats in the Atlantic Forest. *Revista Brasileira de Biologia* 56(2). 391-401.

PARKER, T. A. III, STOTZ, D. F., and FITZPATRICK, J. W. 1996. *Ecological and distributional databases.* Pp. 115-436. *In*: Stotz D F, Fitzpatrick J W, Parker T A III, and Moskovits D K (Eds.) Neotropical Birds: Ecology and conservation. University of Chicago Press, Chicago.

PEARMAN, P. B. 2002. The scale of community structure: Habitat variation and avian guilds in tropical forest understory. *Ecological Monographs* 72(1): 19-39.

PEARSON, A. K., PERSON, O. P., and GOMEZ, I. A. 1994. Biology of the bamboo *Chusquea culeou* (Poaceae: Bambusoideae) in southern Argentina. *Vegetatio* 111(2): 93-126.

PEARSON, D. L. 1975 The relation of foliage complexity to ecological diversity of three amazonian bird communities. *Condor* 77: 453-466.

PIZO, M. A. 2002. *The seed-dispersers and fruit syndromes of Myrtaceae in the Brazilian Atlantic Forest*. Pp. 129-143. *In*: Levey, D. J.; Silva, W. R. and Galetti, M. (Eds.) Frugivory and seed dispersal: ecology, evolution and conservation. Wallingford, CABI Publishing.

ROBINSON, S. K. and HOLMES, R. T. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. *Ecology* 63(6): 1918-1931.

ROTENBERRY, J. T. 1985. The role of habitat in avian community composition: Physiognomy or floristics? *Oecologia* 67:213-217.

SABO, S. R. 1980. Niche and habitat relations in subalpine bird communities of the white mountains of new hampshire. *Ecological monographs* 50(2): 241-259.

SICK, H. 1997. *Ornitologia Brasileira*. Editora Nova Fronteira, Rio de Janeiro. 912p.

SMA 2001. *Intervales*. São Paulo: Secretaria do Estado do Meio Ambiente.

SNOW, D. W. 1981. Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13(1): 1-14.

STATISTICA. 1993. *Statistica for windows*. Release 4.2. Statsoft, Inc.

TABARELLI, M. and MANTOVANI, W. 2000. Gap-phase regeneration in a tropical montane forest: The effects of gap structure and bamboo species. *Plant Ecology*148(2): 149-155.

TABARELLI, M., MANTOVANI, W. and PERES, C. A. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation* 91: 119-127.

TER BRAAK, C. J. F. 1986. Canonical correspondece analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.

TERBORGH, J. 1977. Bird species diversity on an Andean elevational gradient. *Ecology* 58: 1007-1019.

TERBORGH, J. 1985. *Habitat selection in Amazonian birds*. Pp.311-338. *In*: Cody, M. L. (ed.) Habitat selection in birds. Academic Press. New York,

TERBORGH, J., ROBINSON, S. K., PARKER ,T. A. III, MUNN, C, A., and PIERPONT, N. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60(2): 213-238.

THIOLLAY, J-M. 1999 a. Responses of an avian community to rain forest degradation. *Biodiversity and Conservation* 8: 513-534.

THIOLLAY, J-M. 1999 b. Frequency of mixed species flocking in tropical forest birds and correlates of predation risk: An intertropical comparison. *Journal of Avian Biology* 30(3): 282-294.

TURNER, I. M. 1996. Species loss in fragments of tropical rain forest: A review of the evidence. *Journal of Applied Ecology* 33(2): 200-209.

WEBB, E. L., STANFIELD, B. J., and JENSEN, M. L. 1999. Effects of topography on rainforest tree community structure and diversity in American Samoa, and implications for frugivore and nectarivore populations. *Journal of Biogeography* 26: 887-897.

WHEELWRIGHT, N. T., HABER, W. A., MURRAY, K. G., and GUINDON, C. 1984. Tropical fruit-eating birds and their food plants: a survey of Costa Rican lower montane forest. *Biotropica* 16(3): 173-192.

WIENS, J. A. 1989. *The ecology of bird communities, Vol.1. Foundations and patterns*, Cambridge University Press, Cambridge. 539p.

WIENS, J. A., and ROTENBERRY, J. T. 1981. Habitat associations and community structure of birds in shrub steppe environments. *Ecological Monographs* 51(1): 21-42.

WILLIS, E. O. 1979. The composition of avian communities in remanescent woodlots in Southern Brazil. *Papéis Avulsos de Zoologia* 33 (1): 1-25.

WILLSON, M. F. 1974 Avian community organization and habitat structure. *Ecology* 55:1017-1029.

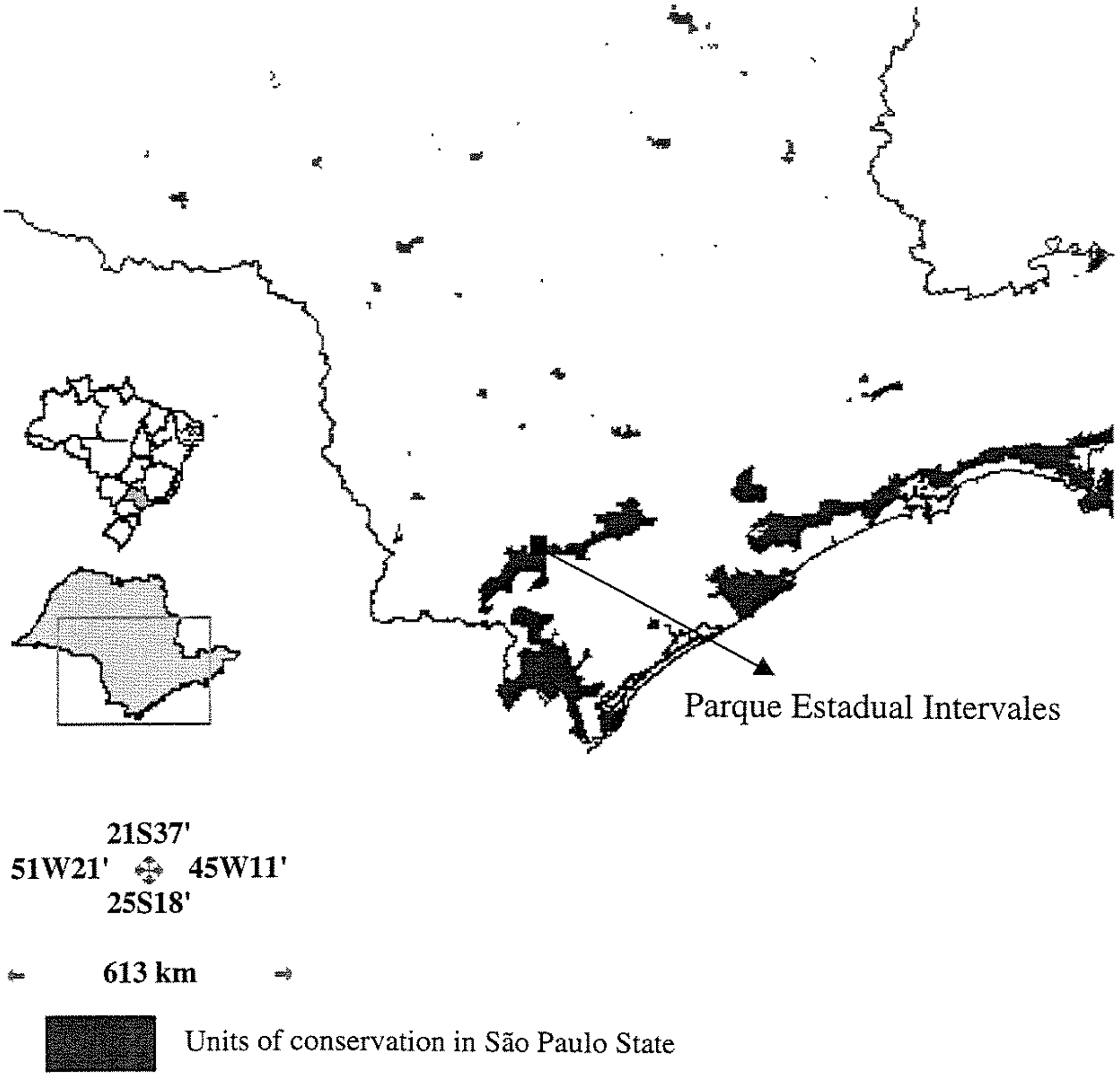

Fig. 1. 1. Localization of Parque Estadual Intervales in southern São Paulo State.

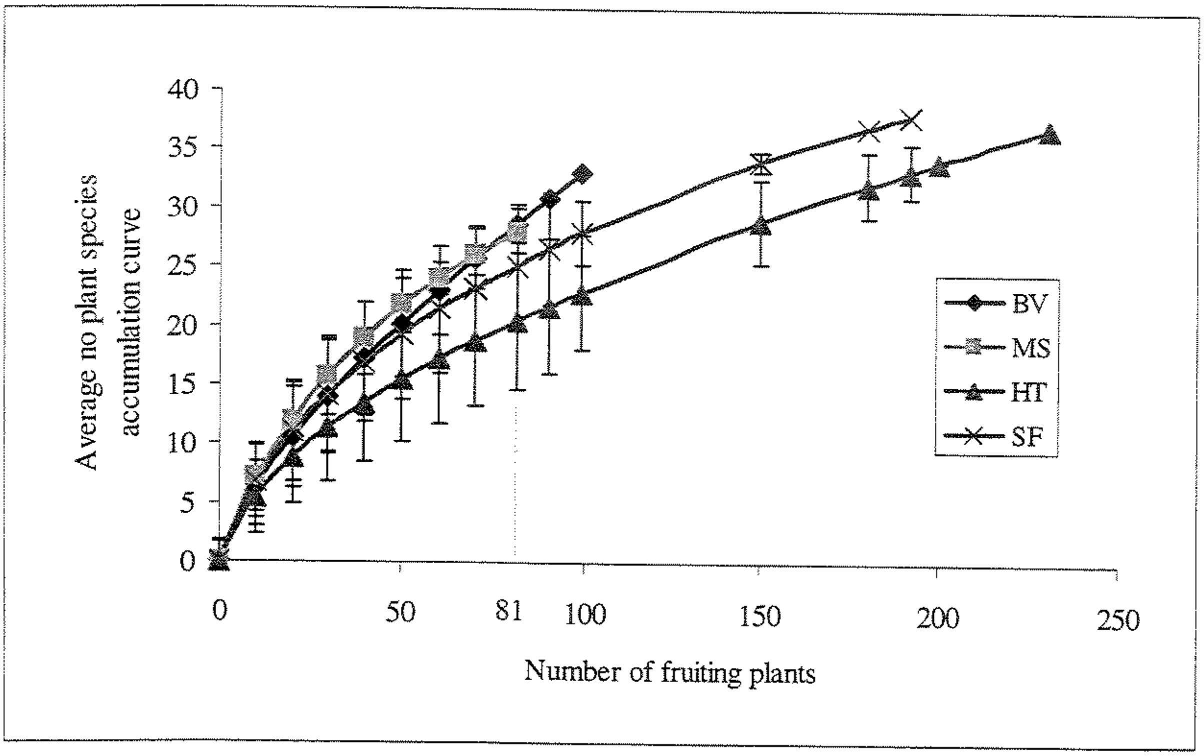

Fig. 1. 2. Average number of fruiting plant species accumulation curve on four different physiognomies: Bottom of valley (BV), Middle slope (MS), Hilltop (HT) and Secondary forest (SF) in Parque Estadual Intervales in southern São Paulo State.

Table 1. 1. Mean and 95% CI for number of species, in 81 individuals of fruiting plants sampled on four different physiognomies: Bottom of valley (BV), Middle slope (MS), Hilltop (HT) and Secondary forest (SF) in Parque Estadual Intervales in southern São Paulo State. Based on 100 simulations. Means are considered different if CIs do not overlap.

Physiognomy	Average richness	95%Conf.Low	95%Conf.High
BV	28.54	25.38	31.71
HT	20.40	15.78	25.02
MS	28.00	28.00	28.00
SF	25.06	20.60	29.52

Table 1. 2. Similarity index (Sorensen) for fruiting plant species sampled on four different physiognomies: Bottom of valley (BV), Middle slope (MS), Hilltop (HT) and Secondary forest (SF) in Parque Estadual Intervales in southern São Paulo State.

	BV	MS	HT	SF
Species richness (S)	34	31	37	38
Total number of sampled individuals	99	102	231	192
Sorensen index (Cs)				
BV		0.34	0.20	0.28
MS			0.21	0.20
HT				0.13

Table 1. 3. Manova analyses considering four habitats with five replica and vegetation structure and plant habit variables. Plant habit was divided into two groups due to statistical limitation of the program.

Manova : factor habitat type					
Principal variables	**Wilks' Lambda**	**Rao's R**	**df 1**	**df 2**	**p-level**
Structure (6 partial variables)	0.027	4.564	18	31	**0.0001**
Plant habit a (4 partial variables)	0.023	9.175	12	34	**0.0000**
Plant habit b (4 partial variables)	0.115	3.648	12	34	**0.0015**
Phenology (3 partial variables)	0.147	4.561	9	34	**0.0005**

Table 1. 4. Specific effect of the structural and plant habit and phenological partial variables.

Specific effect of variables		**F df (1,2)**		
Principal variables	**Partial variables**	**3,16**	**p-level**	**Tukey (p<0.05)**
Structure	Density	31.57	**<0.001**	SF>MS=HT>BV
	Bole	7.17	**0.003**	SF=HT>BV=MS
	Height	9.83	**0.001**	SF=HT>BV=MS
	Total basal area	0.30	0.822	
	Canopy	4.40	**0.019**	SF=MS=HT>BV
	Plant basal area	9.94	**0.001**	SF=HT>BV=MS
Plant habit a(4)	Tree	31.140	**<0.001**	SF=HT>MS>BV
	Shrub	9.685	**0.001**	SF>BV=MS=HT
	Liana	4.715	**0.015**	SF=BV=MS>HT
	Herb	13.383	**<0.001**	SF>BV=MS=HT
Plant habit b(4)	Dead plant	3.459	**0.041**	SF=HT>BV=MS
	Fern	0.773	0.526	
	Palm	14.246	**<0.001**	BV>SF=MS=HT
	Bamboo	2.510	0.096	
Phenology data	No species	5.384	**0.009**	HT=SF=BV>MS
	No fruiting plants	3.177	**0.053**	SF=BV=HT>MS
	Index fruit abundance	0.503	0.686	

Table 1. 5. Median and average of vegetation structure and plant habit variables on four different physiognomies: Bottom of valley (BV), Middle slope (MS), Hilltop (HT) and Secondary forest (SF) in Parque Estadual Intervales in southern São Paulo State.

Vegetation data	**Physiognomies** **SF**	**BV**	**MS**	**HT**
Average of density (ind/m²)	1.179	0.561	0.778	0.895
Median of bole (m)	2.00	4.00	4.00	3.00
Median of height (m)	2.70	6.00	5.00	4.00
Average of total basal area (m²/m²)	0.0060	0.0052	0.0061	0.0049
Median of canopy depth (m)	1.00	0.50	1.00	1.00
Median of ind. basal area (m)	0.0004	0.0016	0.0010	0.0008
Average of density of trees (ind/m²)	0.788	0.328	0.553	0.788
Average of density of shrub (ind/m²)	0.103	0.015	0.009	0.007
Average od density of liana (ind/m²)	0.080	0.072	0.045	0.008
Average of density of herb (ind/m²)	0.088	0.005	0.002	<0.00001
Average of density of dead plant (ind/m²)	0.039	0.017	0.013	0.045
Average of density fern (ind/m²)	0.043	0.018	0.033	0.010
Average of density of palm (ind/m²)	0.010	0.091	0.035	0.028
Average of density of bamboo (ind/m²)	0.030	0.016	0.088	0.011
Median of no of fruiting plant species (med/ m²)	0.0040	0.0027	0.0013	0.0027
Median of no of fruiting plant (med/ m²)	0.0050	0.0040	0.0013	0.0067
Median of fruit abundance index (med/ m²)	0.0110	0.0160	0.0047	0.0140

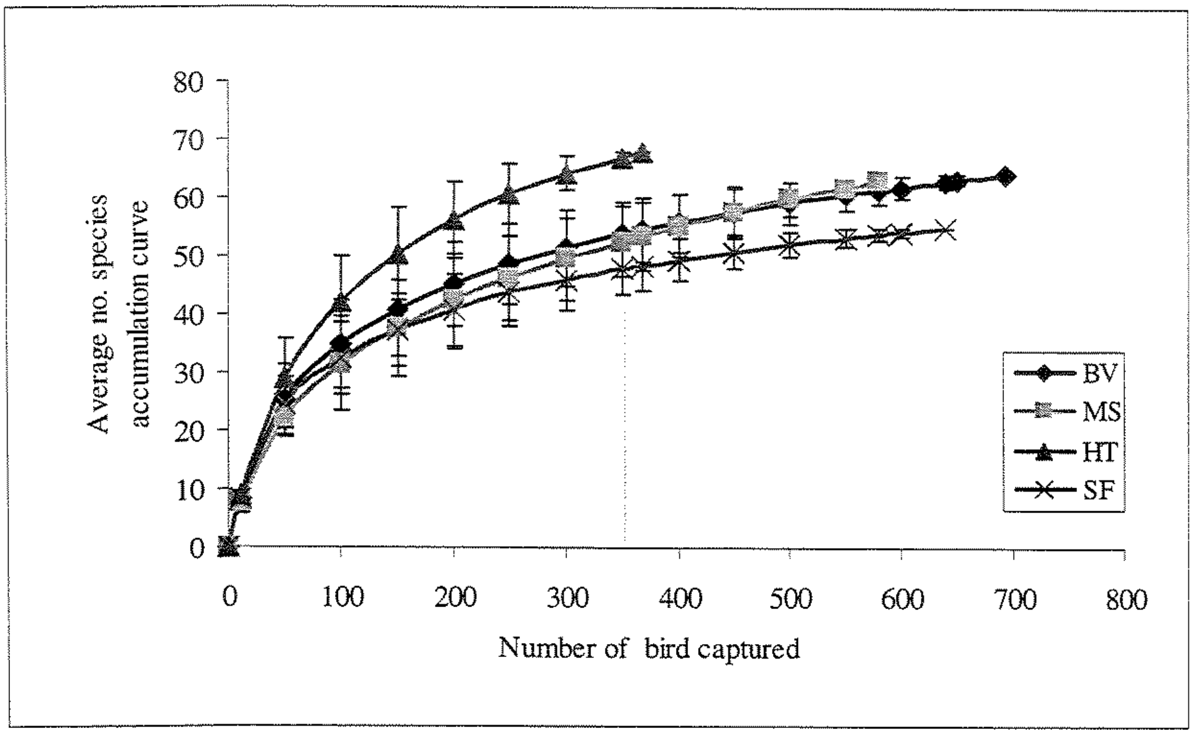

Fig. 1. 3. Average number of bird species accumulation curve on four different physiognomies: Bottom of valley (BV), Middle slope (MS), Hilltop (HT) and Secondary forest (SF) in Parque Estadual Intervales in southern São Paulo State.

Table 1. 6. Mean and 95% CI for number of species in 350 captures on four different physiognomies: Bottom of valley (BV), Middle slope (MS), Hilltop (HT) and Secondary forest (SF) in Parque Estadual Intervales in southern São Paulo State. Based on 100 simulations. Means are considered different if CIs do not overlap.

Physiognomy	**Average richness**	**95%Conf.Low**	**95%Conf.High**
BV	53.69	49.05	58.33
HT	67.06	65.18	68.95
MS	52.52	47.69	57.35
SF	47.77	43.67	51.87

Table 1. 7. Similarity index (Sorensen) for birds captured on four different physiognomies: Bottom of valley (BV), Middle slope (MS), Hilltop (HT) and Secondary forest (SF) in Parque Estadual Intervales in southern São Paulo State.

	BV	**MS**	**HT**	**SF**
Species richness	64	63	68	55
Number of captures	693	579	368	640
Sorensen index (Cs)				
BV		0.66	0.56	0.64
MS			0.61	0.64
HT				0.50

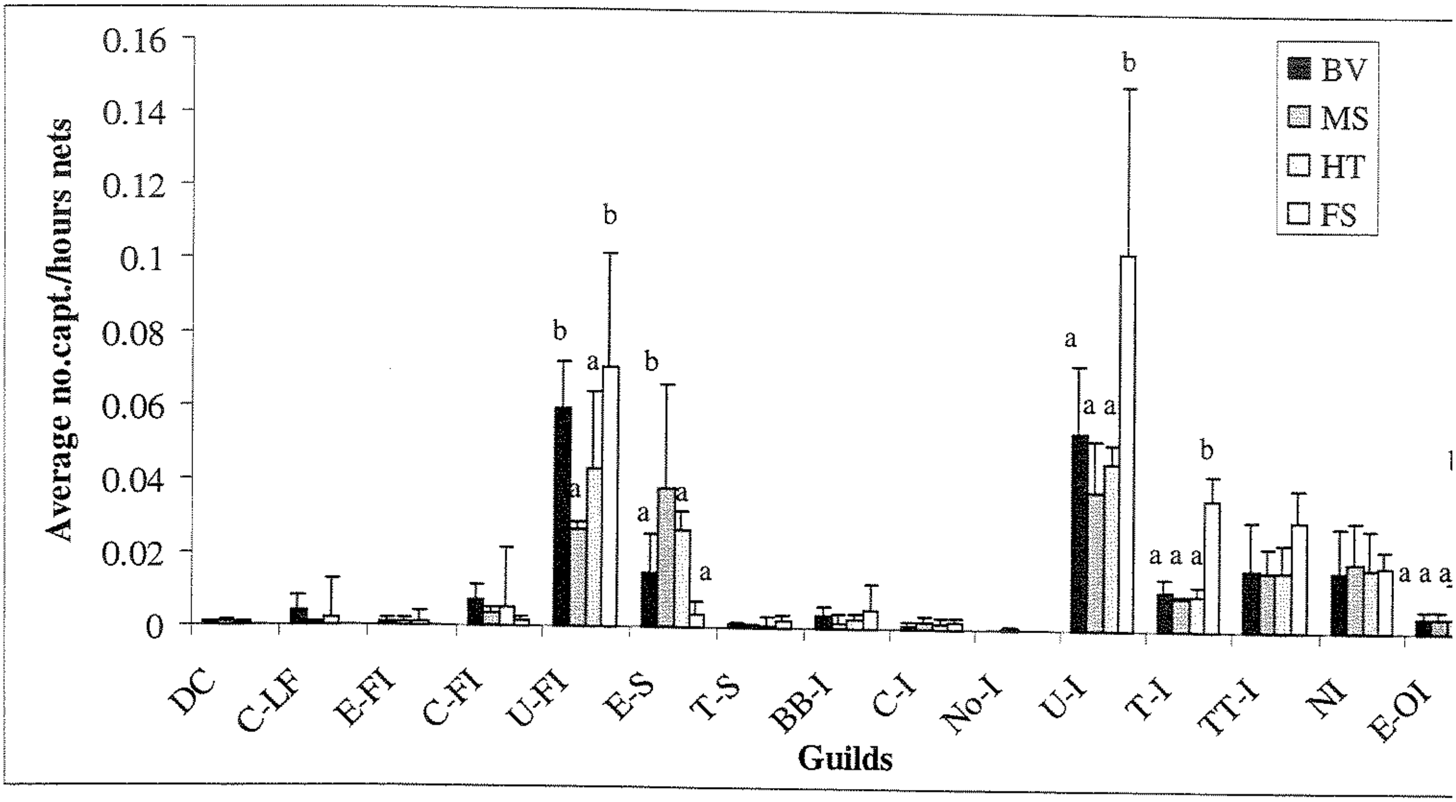

Fig. 1. 4. Average of number of captures of each guild per net-hour in four physiognomies: Bottom of valley (BV), Middle slope (MS), Hilltop (HT) and Secondary forest (SF) in Parque Estadual Intervales in southern São Paulo State. Different letters in each guild shows significant differences among physiognomies: (Anova, $p < 0.05$; Tukey, $p<0.05$).

Guilds: diurnal carnivores (DC), large canopy frugivores (C-LF), edge frugivores/insectivores (E-FI), canopy frugivores/insectivores (C-FI), understory frugivores/insectivores (U-FI), edge seedeaters (E-S), terrestrial seedeaters (T-S), bamboo insectivores (BB-I), canopy insectivores (C-I), nocturnal insectivores (No-I), understory insectivores (U-I), terrestrial insectivores (T-I), trunk and twig insectivores (TT-I), nectarivores/insectivores (NI), edge omnivores/insectivores (E-OI).

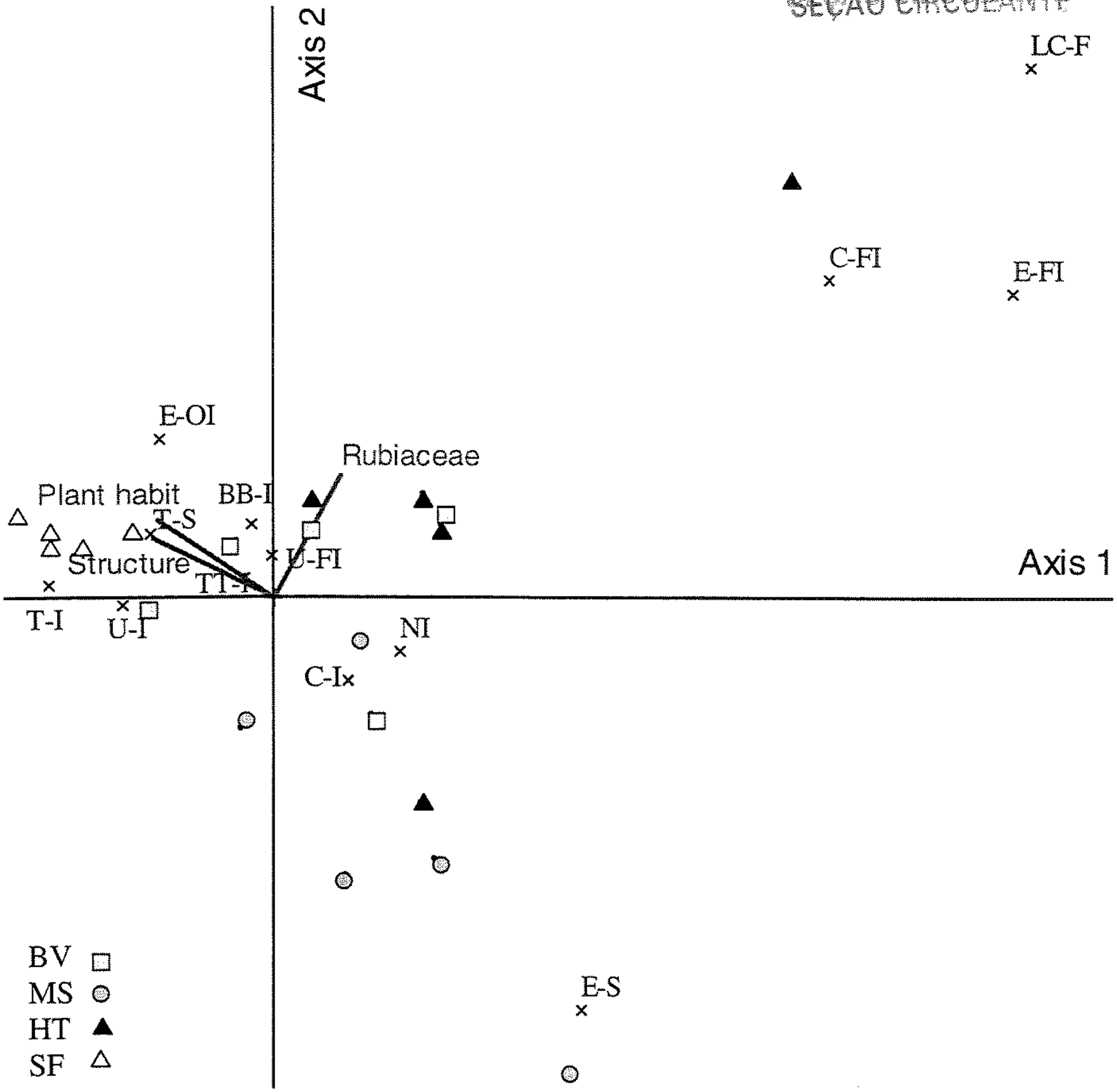

Fig. 1. 5. Biplot of canonical correspondence analyses (CCA) of number of birds captured within guilds in 20 unit samples distributed on four different physiognomies: Bottom of valley (BV), Middle slope (MS), Hilltop (HT) and Secondary forest (SF) in Parque Estadual Intervales in southern São Paulo State. Nine vegetation variables (structure 1, plant habit 1, phenology 1, total basal area, density of bamboo, density of Lauraceae, Melastomataceae, Myrtaceae and Rubiaceae) were considered to correlate the bird capture. Codes for guilds as in Fig. 1. 4. For a detailed comprehension of statistical results see appendix 1. 3.

Table 1. 8. Multiple linear regression among the bird guilds and eight variables of plant habits: tree, shrub, liana, herb, dead plant, palm, fern and bamboo. The principal variables that influenced in a significant way are showed in bold on the table. Codes for guilds as in Fig. 1. 4, n. was the number of units with birds captured in the guild.

Multiple linear regression - Guilds and plant habits								
Guild	**n.**	**r^2**	**F df (11,8)**	**p**	**Principal variables (t, p< 0.05)**	**B**	**t**	**p**
DC	5	0.353	0.75	0.651				
C-LF	9	0.613	2.176	0.116				
E-FI	6	0.7	3.214	**0.038**	tree	-6.36E-03	-2.946	**0.013**
					dead plant	5.64E-02	3.509	**0.005**
C-FI	17	0.74	3.907	**0.02**	dead plant	0.351	4.607	**0.001**
U-FI	20	0.713	3.419	**0.031**	fern	0.418	2.817	**0.017**
E-OI	19	0.75	4.118	**0.017**	dead plant* (p=0.087)	0.179	1.88	0.087
E-S	19	0.56	1.747	0.193				
T-S	10	0.43	1.038	0.464				
BB-I	11	0.859	8.406	**0.001**	tree	-7.87E-03	-2.258	**0.045**
					shrub	-5.97E-02	-3.779	**0.003**
					herb	0.128	6.138	**<0.001**
					bamboo	-2.10E-02	-2.29	**0.043**
C-I	13	0.378	0.837	0.59				
U-I	20	0.901	12.58	**<0.001**	herb	0.78	4.413	**0.001**
T-I	18	0.895	11.765	**<0.001**	herb	0.235	3.87	**0.003**
TT-I	20	0.433	1.049	0.458				
NI	20	0.099	0.151	0.994				

Table 1. 9. Multiple linear regression among guilds and five vegetation structure variables: basal area of individuals, total basal area, canopy depth, density of individuals and bole height. The principal variables that influenced in a significant way are showed in bold in the table. Codes for guilds as in Fig. 1. 4, n. was the number of units with birds captured in the guild.

Multiple Linear Regression: guilds and vegetation structure								
Guild	**n.**	**r^2**	**F df (13,6)**	**p**	**Principal variables With p< 0.05**	**B**	**t**	**p**
DC	5	0.28	0.85	0.55				
C-LF	9	0.48	1.997	0.14				
E-FI	6	0.41	1.499	0.25				
C-FI	17	0.32	1.021	0.45				
U-FI	20	0.2	0.536	0.77				
E-OI	19	0.61	3.371	**0.03**	Canopy depth* (p=0.095)	-2.71E-02	-1.8	0.1
E-S	19	0.24	0.667	0.68				
T-S	10	0.25	0.736	0.63				
BB-I	11	0.6	3.269	**0.04**	Total basal area	1.274	3.49	**<0.00**
C-I	13	0.37	1.264	0.34				
U-I	20	0.76	6.761	**<0.001**	Bole	-4.61E-02	-2.18	**0.05**
					Total basal area	10.483	3.65	**<0.00**
					Basal area ind.	73.823	2.55	**0.02**
T-I	18	0.75	6.319	**<0.001**	Density	4.53E-02	3.31	**0.01**
					Bole	-1.59E-02	-2.19	**0.05**
					Canopy depth	-3.45E-02	-2.31	**0.04**
TT-I	20	0.27	0.799	0.59				
NI	20	0.5	2.202	0.11				

Table 1. 10. Multiple linear regression among the guilds and three phenological variables: number of fruiting plants, number of fruiting plant species and fruit abundance index. The principal variables that influenced in a significant way were showed in bold on the table. Codes for guilds as in Fig. 1. 4, n. was the number of units with birds captured in the guild.

Multiple Linear regression: guilds and phenological variables

Guild	**n.**	r^2	**F df(16,3)**	**p**	**Principal variables (t, p< 0.05)**	**B**	**t**	**p**
DC	5	0.114	0.689	0.572				
C-LF	9	0.229	1.58	0.233				
E-FI	6	0.125	0.765	0.53				
C-FI	17	0.246	1.742	0.199				
U-FI	20	0.156	0.988	0.423				
E-OI	19	0.295	2.228	0.124				
E-S	19	0.246	1.744	0.198				
T-S	10	0.035	0.192	0.9				
BB-I	11	0.28	2.074	0.144				
C-I	13	0.218	1.488	0.256				
U-I	20	0.213	1.446	0.267				
T-I	18	0.388	3.383	**0.044**	no. plant spp	7.826	3.03	**0.008**
					no. fruiting plants	-5.04	-2.4	**0.029**
TT-I	20	0.043	0.237	0.869				
NI	20	0.269	1.96	0.161				

Appendix 1. 1. Number and percentage of bird captures on four different physiognomies: Bottom of valley (BV), Middle slope (MS), Hilltop (HT) and Secondary forest (SF) in Parque Estadual Intervales in southern São Paulo State. Codes for guilds as in Fig.1.4. (classification following Sick, 1997).

nilies	**Species**		**BV**		**MS**		**HT**		**SF**	
		Guild	**N**	**%**	**N**	**%**	**N**	**%**	**N**	**%**
amidae	*Crypturellus obsoletus*	T-S					1	0.27		
cipitridae	*Accipiter poliogaster*	D-C			1	0.17				
conidae	*Micrastur ruficollis*	D-C	1	0.14	2	0.35	1	0.27		
lumbidae	*Geotrygon montana*	T-S	2	0.29	1	0.17	3	0.82		
lumbidae	*Leptotila rufaxilla*	T-S							4	0.6
lumbidae	*Leptotila verreauxi*	T-S	2	0.29			1	0.27		
igidae	*Glaucidium minutissimum*	No-I			1	0.17				
ochilidae	*Amazilia versicolor*	NI	3	0.43			4	1.09	3	0.4
ochilidae	*Clytolaema rubricauda*	NI	2	0.29	12	2.07	4	1.09	2	0.3
ochilidae	*Leucochloris albicollis*	NI					1	0.27		
ochilidae	*Melanotrochilus fuscus*	NI	8	1.15	1	0.17			2	0.3
ochilidae	*Phaethornis eurynome*	NI	20	2.89	28	4.84	14	3.80	14	2.1
ochilidae	*Phaethornis pretrei*	NI	1	0.14						
ochilidae	*Phaethornis squalidus*	NI	2	0.29					4	0.6
ochilidae	*Ramphodon naevius*	NI	2	0.29						
ochilidae	*Thalurania glaucopis*	NI	20	2.89	27	4.66	19	5.16	14	2.1
ogonidae	*Trogon rufus*	C-FI	5	0.72	4	0.69	4	1.09		
ogonidae	*Trogon surrucura*	C-FI					2	0.54		
omotidae	*Baryphthengus ruficapillus*	U-FI	6	0.87	1	0.17				
cconidae	*Malacoptila striata*	U-I	1	0.14						
cconidae	*Nonnula rubecula*	U-I	1	0.14						
mphastidae	*Baillonius bailloni*	C-LF	4	0.58						
mphastidae	*Ramphastos dicolorus*	C-LF					6	1.63		
mphastidae	*Selenidera maculirostris*	C-LF	3	0.43			2	0.54		
cidae	*Celeus flavescens*	TT-I	1	0.14						
cidae	*Picumnus cirratus temminckii*	TT-I							5	0.7
cidae	*Veniliornis spilogaster*	TT-I			1	0.17				
endrocolaptidae	*Campylorhamphus falcularius*	TT-I					1	0.27		
endrocolaptidae	*Dendrocincla fuliginosa turdina*	U-I	28	4.04	1	0.17	1	0.27		
endrocolaptidae	*Dendrocolaptes platyrostris*	U-I	6	0.87	7	1.21	8	2.17	2	0.3
endrocolaptidae	*Lepidocolaptes fuscus*	TT-I	22	3.17	14	2.42	11	2.99	34	5.3
endrocolaptidae	*Lepidocolaptes squamatus*	TT-I			3	0.52				
endrocolaptidae	*Sittasomus griseicapillus*	TT-I	28	4.04	30	5.18	25	6.79	18	2.8
endrocolaptidae	*Xiphocolaptes albicollis*	TT-I	1	0.14	2	0.35	6	1.63	1	0.1
rnariidae	*Anabacerthia amaurotis*	U-I							11	1.7

Families	**Species**		**BV**		**MS**		**HT**		**SF**
		Guild	**N**	**%**	**N**	**%**	**N**	**%**	**N**
Furnariidae	*Anabazenops fuscus*	BB-I	11	1.59	1	0.17	3	0.82	4
Furnariidae	*Automolus leucophthalmus*	U-I	9	1.30	1	0.17			4
Furnariidae	*Cichlocolaptes leucophrys*	C-I	1	0.14	6	1.04			1
Furnariidae	*Heliobletus contaminatus*	C-I			2	0.35	4	1.09	1
Furnariidae	*Lochmias nematura*	T-I			5	0.86			1
Furnariidae	*Philydor atricapillus*	U-I	17	2.45	9	1.55			
Furnariidae	*Philydor lichtensteini*	TT-I	1	0.14					1
Furnariidae	*Philydor rufus*	C-I	2	0.29					
Furnariidae	*Sclerurus scansor*	T-I	9	1.30	9	1.55			9
Furnariidae	*Synallaxis cinerascens*	U-I	1	0.14					
Furnariidae	*Synallaxis ruficapilla*	BB-I	2	0.29	1	0.17			6
Furnariidae	*Syndactyla rufosuperciliata*	TT-I	7	1.01	8	1.38	8	2.17	6
Furnariidae	*Xenops minutus*	TT-I			1	0.17			
Furnariidae	*Xenops rutilans*	TT-I					1	0.27	
Formicariidae	*Chamaeza campanisona*	T-I	4	0.58	4	0.69	2	0.54	4
Formicariidae	*Formicarius colma*	T-I			1	0.17			
Formicariidae	*Grallaria varia*	T-I			1	0.17			
Formicariidae	*Thamnophilus caerulescens*	E-OI					3	0.82	1
Thamnophilidae	*Batara cinerea*	BB-I			2	0.35			
Thamnophilidae	*Drymophila ferruginea*	U-I			1	0.17			
Thamnophilidae	*Drymophila ochropyga*	BB-I			1	0.17			1
Thamnophilidae	*Dysithamnus mentalis*	U-I	2	0.29	7	1.21	4	1.09	39
Thamnophilidae	*Dysithamnus xanthopterus*	U-I					2	0.54	
Thamnophilidae	*Myrmeciza squamosa*	T-I	6	0.87	8	1.38			25
Thamnophilidae	*Myrmotherula gularis*	U-I	20	2.89	8	1.38	1	0.27	26
Thamnophilidae	*Pyriglena leucoptera*	U-I	35	5.05	35	6.04	6	1.63	54
Conopophagidae	*Conopophaga lineata*	T-I			4	0.69	3	0.82	38
Conopophagidae	*Conopophaga melanops*	T-I	14	2.02	1	0.17	2	0.54	
Cotingidae	*Carpornis cucullatus*	C-LF			1	0.17	14	3.80	
Cotingidae	*Lipaugus lanioides*	C-LF	7	1.01					
Cotingidae	*Pachyramphus validus*	E-OI	2	0.29			1	0.27	
Cotingidae	*Procnias nudicollis*	C-LF					1	0.27	
Cotingidae	*Tityra cayana*	C-FI					6	1.63	
Pipridae	*Chiroxiphia caudata*	U-FI	25	3.61	14	2.42	15	4.08	35
Pipridae	*Ilicura militaris*	U-FI	2	0.29	1	0.17	7	1.90	
Pipridae	*Schiffornis virescens*	U-FI	10	1.44	19	3.28	14	3.80	19
Tyrannidae	*Atilla phoenicurus*	C-I							2
Tyrannidae	*Atilla rufus*	E-OI			1	0.17	5	1.36	2

milies	Species	Guild	BV N	%	MS N	%	HT N	%	SF N	%
rannidae	*Camptostoma obsoletum*	E-OI					1	0.27		
rannidae	*Elaenia mesoleuca*	E-FI	4	0.58	3	0.52	3	0.82		
rannidae	*Hemitriccus obsoletus*	U-I			10	1.73	15	4.08		
rannidae	*Lathrotriccus euleri*	U-I			2	0.35			10	1.
rannidae	*Leptopogon amaurocephalus*	U-I	9	1.30	2	0.35			8	1.
rannidae	*Mionectes rufiventris*	U-FI	25	3.61	12	2.07	24	6.52	6	0.
rannidae	*Myarchus swainsoni*	C-FI			2	0.35	6	1.63		
rannidae	*Myiobius barbatus*	U-I	11	1.59					3	0.
rannidae	*Myiodynastes maculatus*	C-FI					1	0.27		
rannidae	*Myiornis auricularis*	E-OI	1	0.14						
rannidae	*Neopelma aurifrons*	U-FI							2	0.
rannidae	*Onychorhynchus coronatus*	U-I	4	0.58	2	0.35	3	0.82	1	0.
rannidae	*Phyllomyias virescens*	E-OI							1	0.
rannidae	*Phylloscartes oustaleti*	C-I	1	0.14						
rannidae	*Phylloscartes ventralis*	C-I					1	0.27		
rannidae	*Platyrinchus mystaceus*	U-I	47	6.78	51	8.81	12	3.26	41	6.
yruncidae	*Oxyruncus cristatus*	C-FI					2	0.54		
uscicapidae	*Platycichla flavipes*	C-FI	17	2.45	3	0.52	6	1.63		
uscicapidae	*Turdus albicollis*	U-FI	29	4.18	20	3.45	4	1.09	28	4.
uscicapidae	*Turdus leucomelas*	E-OI					2	0.54		
uscicapidae	*Turdus rufiventris*	E-OI	1	0.14	2	0.35			6	0.
uscicapidae	*Turdus subalaris*	C-FI	1	0.14						
ireonidae	*Cyclarhis gujanensis*	C-FI					1	0.27	1	0.
ireonidae	*Hylophilus poicilotis*	U-FI							4	0.
ireonidae	*Vireo chivi*	E-OI							1	0.
rulidae	*Basileuterus culicivorus*	E-OI	4	0.58	10	1.73	4	1.09	21	3.
rulidae	*Basileuterus leucoblepharus*	U-I	1	0.14			2	0.54	23	3.
rulidae	*Basileuterus rivularis*	T-I	5	0.72						
mberizidae	*Arremon flavirostris*	BB-I			1	0.17				
mberizidae	*Cacicus chrysopterus*	U-FI					1	0.27		
mberizidae	*Euphonia pectoralis*	C-FI	2	0.29	3	0.52	5	1.36	2	0.
mberizidae	*Habia rubica*	U-FI	43	6.20	3	0.52			21	3.
mberizidae	*Haplospiza unicolor*	E-S	53	7.65	137	23.66	26	7.07	8	1.
mberizidae	*Orthogonys chloricterus*	C-FI			1	0.17	1	0.27		
mberizidae	*Pipraeidea melanonota*	E-OI					1	0.27		
mberizidae	*Saltator similis*	E-OI							2	0.
mberizidae	*Stephanophorus diadematus*	E-FI					2	0.54		
mberizidae	*Tachyphonus coronatus*	E-OI	6	0.87			3	0.82	21	3.
mberizidae	*Tangara cyanocephala*	C-FI					1	0.27		

Families	**Species**		**BV**		**MS**		**HT**		**SF**
		Guild	**N**	**%**	**N**	**%**	**N**	**%**	**N**
Emberizidae	*Tangara desmaresti*	C-FI					5	1.36	
Emberizidae	*Thraupis cyanoptera*	E-OI			1	0.17	3	0.82	
Emberizidae	*Thraupis ornata*	C-FI					3	0.82	
Emberizidae	*Tiaris fuliginosa*	E-OI					1	0.27	
Emberizidae	*Trichothraupis melanops*	U-FI	73	10.53	26	4.49	13	3.53	37
Total	**117**		**693**	**100.0**	**579**	**100.0**	**367**	**100.0**	**640**

Appendix 1. 2. Principal component analysis (PCA): matrix of weighted correlations between the variables used in PCA and each axis with the eigenvalue value.

Appendix 1. 2 a. Vegetation structure

Factor Loadings (Unrotated) (pca-est.sta)
Extraction: Principal components
(Marked loadings are > .700000)

	Factor 1	**Factor 2**	**Factor 3**	**Factor 4**	**Factor 5**
Eigenval	3.786	1.196	0.591	0.329	0.067
% total variance	63.095	19.934	9.855	5.479	1.125
Cumul. Eigenval	3.786	4.982	5.573	5.902	5.969
Cumul. %	63.095	83.029	92.884	98.363	99.488
Density	0.864	-0.272	0.064	0.397	-0.131
Bole	-0.928	-0.199	-0.023	0.282	0.084
Plant height	-0.917	-0.288	-0.168	0.175	0.030
Total basal area	-0.005	-0.936	0.287	-0.203	-0.002
Canopy depth	0.665	-0.351	-0.655	-0.064	0.043
Plant basal area	-0.946	-0.016	-0.218	-0.126	-0.201
Expl.Var	3.786	1.196	0.591	0.329	0.067
Prp.Totl	0.631	0.199	0.099	0.055	0.011

Appendix 1. 2 b. Plant habits

Factor Loadings (Unrotated) (pca-life.sta)
Extraction: Principal components
(Marked loadings are > .700000)

	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Eigenval	2.744	1.770	1.200	0.848	0.697
% total variance	34.299	22.127	14.996	10.594	8.718
Cumul. Eigenval	2.744	4.514	5.714	6.561	7.259
Cumul. %	34.299	56.426	71.422	82.016	90.734
Tree	0.613	0.620	-0.003	-0.024	-0.339
Shrub	0.785	-0.402	0.062	-0.158	-0.198
Liana	0.378	-0.731	0.060	0.369	0.287
Herb	0.819	-0.335	-0.071	0.267	-0.267
Dead plant	0.592	0.399	-0.276	0.052	0.588
Fern	0.167	-0.213	0.811	-0.458	0.164
Palm	-0.706	-0.517	-0.242	0.025	-0.125
Bamboo	-0.246	0.325	0.629	0.633	-0.042
Expl.Var	2.744	1.770	1.200	0.848	0.697
Prp.Totl	0.343	0.221	0.150	0.106	0.087

Appendix 1. 2 c. Phenological data.

Factor Loadings (Unrotated) (pca-fen.sta)
Extraction: Principal components
(Marked loadings are > .700000)

	Factor 1	Factor 2	Factor 3
Eigenval	2.255	0.581	0.164
% total variance	75.170	19.356	5.473
Cumul. Eigenval	2.255	2.836	3.000
Cumul. %	75.170	94.527	100.000
No. fruiting plant species	0.807	-0.568	-0.160
No. fruiting plants	0.949	0.036	0.313
Index fruit abundance	0.838	0.506	-0.201
Expl.Var	2.255	0.581	0.164
Prp.Totl	0.752	0.194	0.055

Appendix 1. 3. Tables of canonical correspondence analysis (CCA) of guild species with vegetation structure, plant habit, plant composition and phenological data variables in each unit sampled.

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AXIS SUMMARY STATISTICS
Number of canonical axes: 3
Total variance ("inertia") in the species data:   0.4523
-----------------------------------------------------------
                                    Axis 1   Axis 2   Axis 3
-----------------------------------------------------------
Eigenvalue                           0.147    0.093    0.026
Variance in species data
     % of variance explained          32.5     20.6      5.8
     Cumulative % explained           32.5     53.1     58.9
Pearson Correlation, Spp-Envt*       0.953    0.834    0.900
Kendall (Rank) Corr., Spp-Envt       0.705    0.463    0.726
-----------------------------------------------------------
* Correlation between sample scores for an axis derived from the species
     data and the sample scores that are linear combinations of the
     environmental variables. Set to 0.000 if axis is not canonical.


MONTE CARLO TEST RESULTS -- EIGENVALUES
-----------------------------------------------------------
                               Randomized data
            Real data    Monte Carlo test,   99 runs
           ------------  ------------------------
  Axis      Eigenvalue   Mean     Minimum   Maximum        p
-----------------------------------------------------------
     1         0.147     0.107     0.051     0.142    0.0100
     2         0.093     0.061     0.024     0.110    0.0800
     3         0.026     0.022     0.014     0.032    0.1300
-----------------------------------------------------------
p = proportion of randomized runs with eigenvalue greater
    than or equal to the observed eigenvalue; i.e.,
p = (1 + no. permutations >= observed)/(1 + no. permutations)


MONTE CARLO TEST RESULTS -- SPECIES-ENVIRONMENT CORRELATIONS
-----------------------------------------------------------
                               Randomized data
            Real data    Monte Carlo test,   99 runs
           ------------  ------------------------
  Axis   Spp-Envt Corr.  Mean     Minimum   Maximum       p
-----------------------------------------------------------
    1        0.953     0.837     0.650     0.976    0.0500
    2        0.834     0.683     0.546     0.935    0.0700
    3        0.900     0.829     0.578     0.939    0.1600
-----------------------------------------------------------
p = proportion of randomized runs with species-environment
    correlation greater than or equal to the observed
    species-environment correlation; i.e.,
p = (1 + no. permutations >= observed)/(1 + no. permutations)
```

```
CORRELATIONS AND BIPLOT SCORES for   9 variable
-----------------------------------------------------------------------------
                            Correlations*             Biplot Scores
   Variable              Axis 1  Axis 2  Axis 3    Axis 1  Axis 2  Axis 3
---------------------------------------------------------------------
  1 structure1           -0.592   0.391   0.461    -0.592   0.391   0.461
  2 tot.basal area       -0.338  -0.053   0.092    -0.338  -0.053   0.092
  3 Lauraceae            -0.239  -0.222   0.194    -0.239  -0.222   0.194
  4 Melastomataceae       0.321  -0.336   0.260     0.321  -0.336   0.260
  5 Myrtaceae            -0.170   0.318   0.374    -0.170   0.318   0.374
  6 Rubiaceae             0.331   0.796   0.127     0.331   0.796   0.127
  7 phenology            -0.195   0.472   0.145    -0.195   0.472   0.145
  8 plant habit            -0.575   0.501   0.270    -0.575   0.501   0.270
  9 bamboo                0.067  -0.529   0.386     0.067  -0.529   0.386
------------------------------------------------------------------------------
* Correlations are "intraset correlations" of ter Braak (1986)
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CAPÍTULO 2

NICHE BREADTH OF FRUGIVOROUS BIRDS IN ATLANTIC FOREST, BRAZIL: INFLUENCE OF MORPHOLOGICAL AND NUTRITIONAL TRAITS ON FRUIT SELECTION

NICHE BREADTH OF FRUGIVOROUS BIRDS IN ATLANTIC FOREST, BRAZIL: INFLUENCE OF MORPHOLOGICAL AND NUTRITIONAL TRAITS ON FRUIT SELECTION

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ABSTRACT

Fruit preference by birds is a complex process based up the morphology and nutritional traits of fruits and on physiological needs and capabilities of birds. To investigate the variation on fruit preference among bird species and establish some selection patterns associated with bird morphology, we examined simultaneously plant species richness, morphological and nutritional composition of fruits in order to characterize the feeding strategies and analyze the food selection by 31 frugivorous birds over three years in the Atlantic Forest of southeast Brazil. In general, birds eat a high diversity of fruit species; but at the same time, they show clear preference and select fruits according to morphological and nutritional traits and with high species richness. The fruit morphological specialization tend to be associated directly with bird mass, but not with a strong correlation because the birds are capable to overcoming constraints imposed by fruit size with a complexity feeding behavior. In relation of fruit selection, the larger birds selected preferentially fruits with larger seed mass and size and while the smaller birds selected fruits with small seeds mass and size. In contrast with the high morphological specialization, the general pattern observed for nutritional composition is a generalist feeding strategy. It seems to suggest that the strong nutritional imbalance characterizing the pulp of most fruit species should force frugivores to have mixed-species diets with high variation on nutritional content in order to get a balanced input of energy, protein, vitamins, and minerals. The bird species showed a wide flexibility concerning the nutritional fruit traits but not with the same nutritional requirement. The fruit species richness consumed by birds was not associated with bird size and neither with morphological and/or nutritional traits of fruit consumed. These results may have evolutionary implications in the plant/frugivore mutualisms.

***Key words*:** niche breadth, frugivore, bird, nutritional composition, morphology, fruit, species richness, feeding strategy, Atlantic Forest, Brazil, Tropical Rain Forest.

INTRODUCTION

The ecological niche of a species has been defined as a region of *n*-dimensional hyper-space, that represents all the biotic and abiotic factors that influence individuals of that species (Hutchinson 1957 *apud* Pianka 1988). To determine the niche of a species, one must not only investigate where the species carries on its activities (e.g., feeding, nesting) but also find out the kinds of food it requires. For frugivorous birds, differences in fruit choice patterns among species have been attributed to fruit and seed size (Wheelwrigth 1985), fruit color (Greig-Smith 1986, Nakanishi 1996), and chemical composition of pulp (Sun *et al.* 1997, Levey and Cipollini 1998, Witmer and Soest 1998). The bird traits involved in these choice patterns include the gape size (Jordano 1986), digestive physiology (Fuentes 1994) and foraging behavior (Moermond and Denslow 1985). Most studies examined fruit choice patterns focusing on the fruit traits separately. However, all traits may operate simultaneously influencing bird choice. Here, we examined simultaneously plant species richness, morphological and nutritional composition of fruits in order to characterize and analyze the food selection by frugivorous birds in the Atlantic Forest of southeast Brazil, asking the following questions:

1) Are the fruit morphology correlated with body size and bill dimensions of birds?

Usually ecologists think about dietary niche breadth in terms of prey size range. The general pattern observed is that the prey size tends to be directly proportional to the size of the predator, both within and between species (Van Valen and Grant 1970, Anderson and Mathis 1999, Luiselli *et al.* 1998, Sabates and Saiz 2000). Interpretation of such pattern derives from the foraging theory (Schoener 1991). Prey smaller than the predator tend to be ignored or taken less often than intermediate-sized prey due to the increasing difficulty of detection, capture, and or handling with diminishing prey size (Maurer 1996). This relation is supported by studies on granivorous (Willson 1971) and frugivorous birds (Martin 1985, Debussche and Isenmann 1989).

2) Are the body size of birds correlated with the range size and species diversity of fruit consumed?

When the niche breadth is estimated in terms of diversity of prey species consumed, in general the predator body size and its morphological apparatus, like jaw size, tend to correlate with the diversity of prey species and the prey range size (Brandl *et al.* 1994, Churchfield *et al.* 1999). This may be expected due to a certain broad systematic categories that reflect size classes (Schoener and Janzen 1968). However, for frugivorous birds, a different pattern can be found when one considers the classical idea of specialization and generalization among avian frugivores and tropical trees (see details in Snow 1981, Moermond and Denslow 1985, Howe 1993). According to this hypothesis, the frugivores are arranged on a continuum between specialists and generalists. The idea is based on the assumption that reliable attraction of dispersers to large-seeded fruits entails provision of a high quality reward to the bird. Hence, large-seeded fruits are seen to be nutritious and closely linked evolutionarily with highly frugivorous birds that depend on fruits for most of their protein and energy needs (specialist) and whose gape are large enough to handle large seeds. Most of small frugivores (usually with body mass < 50g) are seen as opportunists (generalists) that take fruits nonselectively and are willing to settle for small, juicy, low-reward fruits.

3) Do the nutrients in fruits explain the patterns of fruit choice by birds?

Unfortunately, studies on nutritional requirements of wild frugivorous birds are very scarce. Information about the nutritional needs mainly come from domesticated species (see details in Murphy 1996). In general, it seems reasonable to suggest that wild bird species which share similar dietary habits (e.g. frugivores, nectarivores or insectivores) should have similar nutritional requirements (Murphy 1996).

At the end, the specific goal of this study is to characterize the feeding strategies of 31 frugivorous bird species based on fruit species richness, and two aspects of niche breadth morphology and nutritional composition of fruit selection.

MATERIAL AND METHODS

STUDY AREA

The study was conducted in three sites in the Atlantic Rain Forest of Parque Estadual Intervales (PEI) in southern São Paulo State, southeastern Brazil, between 1999 and 2002 (Fig. 2. 1). The average annual rainfall is 1,500 to 1,800 mm and temperature is 17 to 19°C (SMA 2001). PEI is a 49,000 ha protected area surrounded by three other reserves encompassing a total of 120,000 ha of continuous forest. It is composed of different types of physiognomies partially caused by the variation on elevation gradient (from 60 to 1,100 m a.s.l.), climate and soil (Mantovani 2001). The forest sites are different from each other and are characterized as hilltop, middle slope and bottom of valley (Mantovani *et al.* 1990). The vegetation in these physiognomies is classified as Lower Montane Rain Forest (700-1,100 m a.s.l.), and is considered to be "typical" Atlantic Forest (Oliveira-Filho & Fontes 2000). The hilltop (HT) is located at "Mirante da Anta" (24°16' 42''S and 48° 24' 28''W) at *ca* 1,000 m elevation. The middle slope (MS) is located at "Barra Grande" (24°18'

17''S and 48° 21' 53''W) which elevation is about 900 m. The bottom of valley (BV) is located at "Carmo" (24°18' 60''S and 48° 25' 00''W) with 700 m of elevation.

We selected the localization of three study sites by vegetation type and topographic zone to cover the existing environmental variation in the Atlantic Forest that included hilltop, middle slope and bottom of valley (Mantovani *et al.* 1990). In each site five sample units were established for bird captured with mist nets and foraging observations. Nearest neighbor distance among the units of the same habitat varied from 10 m to 1,000 m and from 8,000 m to 20,000 m between habitats. Because much of the study areas were too rugged to accommodate the mist nets, we were forced to choose sites based on an additional feasibility criterion. These units were determined a priori to produce an independent data set from each habitat type for statistical analyses.

DETERMING BIRD DIETS

We combined two techniques to collect the information of bird diet. The first was the direct observation of the birds foraging behavior; the second was identification of seeds in fecal samples from birds captured in mist nets.

a) *Observation of foraging behavior* - The method used on direct observation was based on feeding bouts (Galetti *et al.* 2000). This method consisted of walking along trails, and every time that a bird was observed feeding, a bout was recorded irrespectively of the time spent feeding. If the bird moved to another plant, a new bout was recorded. During these observations, we recorded the bird and plant species. When the plant was unknown, we collected ripe fruits for morphological and chemical analyses and vegetative parts for future plant identification. Besides the identification of bird species, we recorded the general (habitat types) and the specific localization (vertical stratification) where the foraging behavior occurred and number of individuals as well. We also collected seeds regurgitated or defecated by birds wherever observation was possible. This method, although may overrepresent abundant plant species and conspicuous bird species, was used here because it supplied mist net deficiency on sampling canopy birds (Blake and Loiselle 2000, Blake and Loiselle 2001).

b) *Fecal samples collected in mist nets* - In this technique, birds were captured in five units for each forest site (BV, MS and HT) with 10 mist nets per unit (36 mm mesh, 12 x 2.5 m). We placed the nets in line on these units and each unit were sampled one day each month during one year (total sampled BV=MS=HT=3,600 mist-net-hours). They were open from dawn to early afternoon (6 hours). We checked nets at least once per hour and more than this during rain. The MS were sampled from April 1999 to March 2000, BV from April 2000 to March 2001 and HT from April 2001 to March 2002.

All frugivorous birds were identified and banded with numbered aluminum leg bands. From each bird captured, the following biometric data were collected: body mass and bill length, width and depth. All measurements were made with a caliper nearest to 1.0 mm. After this, the birds were kept in a cloth bag for at least half hour and then were inspected for fecal material; the fecal material was carefully inspected for seeds. The seeds found were identified with the aid of reference collection of seeds taken from ripe fruits collected in the forest sites and were kept in the Laboratório de Interações Vertebrados-Plantas (Unicamp).

CHARACTERIZATION OF PLANT SPECIES CONSUMED

All fruiting plant species presenting bird dispersal syndrome (arillate seeds, drupes or berries; attractive colors or bicolored displays; scentless (*sensu* Pijl 1982)) localized in the sites were identified. We also sampled some fruits with other morphological traits that are potencially consumed by the birds, like *Piper* spp. and *Campomanesia* spp. (Gomes 2001, Pizo 2002). The samples of ripe fruits were collected and the following morphological and nutritional data were obtained: total mass of fruit, seeds and pulp; largest and smallest diameter (length and width) of fruit and seed; number of seeds and percentage (%) of proteins, lipids, soluble sugar and insoluble sugar (Appendix 2. 4). Measurements were made for at least 10 fruits, chosen, when it was possible, from different plants. Chemical analyses were made in the Laboratório de Ecologia Química (Unicamp). Protein was determined according the methods described Jeffery *et al.*, (1989). Lipid content was determined following the methods described by Bligh and Dyer (1959) and soluble and insoluble sugar by Fales (1951), Kearns and Inouye, (1993) and Poorter and Villar (1997).

We used "fruits" in their ecological, and not botanical sense, to denote "functional fruits", i.e., packages made up of seeds plus accessory tissues used as food by birds, irrespective of their anatomical origin (Herrera 1992).

STATISTICAL ANALYSES

CHARACTERIZATION AND COMPARISON OF NICHE BREADTH AMONG BIRD SPECIES

1) Fruit species richness - We estimated the fruit species richness consumed for each bird species using the rarefaction method (Krebs 1999). We calculated rarefaction curve using a Monte Carlo simulation procedure (Ecosim 7.0, Gotelli and Entsminger 2001) that also allows a comparison of the number of plant species expected in the diet of each bird specie on basis of the lowest number of samples recorded among the birds compared; that is, fruit species richness is compared on basis of the same number of samples. Simulations were run 100 times and mean expected number of plant species for each bird species were compared based on the 95% CI with 15, 20 and 30 samples. For clear graphic visualization, we clustered the bird species into four categories according to the rarefaction curve inclination.

For applying this analysis, first of all we organized the records of bird diet (observations and mist net methods) in a quantitative matrix of plant and bird species interactions. We considered one sample record when we found one or more seeds of the same plant species in the fecal sample. If two or more plant species were found in the same fecal sample, another sample record was added to the matrix. For observation of foraging behavior, we considered each feeding bout as one record. Therefore, we obtained a total of 854 fecal samples with seeds collected from 57 bird species and 551 feeding bouts for 64 bird species. When data were combined, we obtained one matrix with 1344 interactions with 69 bird species and 149 plant species. Using the number of plant species in the diet of each bird species, we calculated rarefaction twice, one for all bird species recorded, in order to determine which bird species were adequately sampled in terms of diet characterization, and the other just with bird selected to compare their species richness. From the first rarefaction we selected 31 bird species that consumed 137 plant species with at least 15 samples.

2) **Morphological niche breadth** (MNB) – Multivariate ordination, principal component analysis (PCA), was used in order to measure morphological niche breadth of 31 bird species, considering nine morphological variables of the fruit consumed (total mass of fruit, seeds and pulp; largest and smallest diameter of fruit and seed; number of seeds and mass of one seed). In this analysis, the plant species score is proportional to the weighted mean of the scores and represents the center of the distribution (centroid) what is defined as the niche-position in *n*-dimensional space (Carnes and Slade 1982, Finch 1989). The width of the distribution, as quantified by measures of standard deviation, was used as a measure of niche breadth (Gregory and Gaston 2000). Smaller variances indicate greater specialization in fruit morphology consumed by each bird. As required by PCA, we organized one matrix with 132 plant species eaten by birds and their morphological variables in 9 columns. In function of the huge difference on scales of these variables, the data were transformed by the relativization of plant data by columns totals (Greig-Smith 1983 *apud*

Mccune and Mefford 1999). Additionally, in order to look for patterns of variation in bird diet, we made box plot showing the niche breadth (standard deviation of all the distances of plant specie scores from centroid) for all bird species, which were organized in a body size gradient. To evaluate differences in niche breadth among bird species, we used the one-way factorial anova.

3) **Nutritional niche breadth** (NNB)- For evaluation of niche breadth in terms of four chemical characteristics of the fruits (% of proteins, lipids, soluble sugar and insoluble sugar), we used the same analysis described above without the transformation of the data. The matrix were composed by 117 plant species and 31 bird species. The number of plant species considered in the PCA analyses of morphological and chemical variables differed because fruit samples weren't large enough to allow chemical analyses for some plant species.

CORRELATION AMONG BIRD SPECIES AND FRUIT TRAITS

a) Description of overall patterns of correlations - We used the canonical correspondence analysis (CCA) to describe the relationship between the number of feeding records for 31 bird species and the morphological and chemical fruit variables. CCA is an ordination technique that incorporates multiple regressions, with the ordination axes constrained as linear combinations of morphological and chemical fruit variables. CCA also allows a statistical significance test on the correlation between sample abundance and variables supplied, which is Monte Carlo permutation test (Ter Braak 1986). For applying this analysis, we made two CCA, one for morphological and the other for nutritional fruit data. The morphological data set were organized into two matrices, as required by CCA, and consisted of the feeding records for 31 bird species followed by the mean values of six morphological variables (mass of fruit, seed and pulp, diameter of fruit and seed and number of seed) for the 41 plant families whose fruits were eaten by birds. We used the average of morphological variables of plant families in order to reduce the number of variables. In the same way, the matrix built for the nutritional data set contained the mean values of four variables (% of proteins, lipids, soluble sugar and insoluble sugar) for 29 plant families. CCA graphic results were made emphasizing taxonomic and biometrics relationships between bird species. For the biometrics relationships, the bird species scores on the ordination axis were replaced by their body mass categories. Four categories were defined: small (<20g), medium (20.1 – 40.0g), large (40.1 – 80.0) and very large (> 80.1g).

b) **Specific correlation among niche breadth and biometric bird data.** For this measurement, we applied multiple linear regression to correlate the biometric data of bird species (body mass and bill length, width and depth) with the morphological and chemical fruit characteristics, which represented the niche breadth. We searched for correlation among the dimensions of niche breadth applying Spearman ranking correlation.

DEFINITION OF FEEDING STRATEGIES

We compared different dimensions of niche breadth for bird species transforming the values of morphological and nutritional fruit traits and fruit species richness by the relativization by maximum value of each niche dimension and after plotting these results in a three dimensional graphic.

All these statistical analysis were performed by Statistica Program (1993), PC-ORD 4.10 (Mc Cune and Mefford 1999) and Ecosim 7.0 (Gotelli and Entsminger 2001).

RESULTS

CHARACTERIZATION AND COMPARISON OF NICHE BREADTH AMONG BIRD SPECIES

1) Plant species richness in bird diet

We recorded 137 plant species consumed by 31 frugivorous birds. The average of group species accumulation curves (based on Monte Carlo simulation) indicated that the groups differed in species richness and new species of plants were still being recorded for all groups (Fig 2. .2 and Table 2. 1). At 15 samples, group one (*Cissopis leveriana, Tangara seledon, Orthogonys chloricterus, Orchesticus abeillei, Pipile jacutinga* and *Lipaugus laniodes*) showed a significantly lower species richness than the group three and four. When the number of samples increase for 20 and 30 the group one also differed from some species of group 2 (*Tityra cayana, Platycichla flavipes* and *Tangara cayana*). According to the rarefaction curve inclination, bird species belonging to same family (e.g. Cotingidae, Cracidae) or genus (e.g. *Tangara, Turdus*), showed differences on the inclination rate and therefore were classified on different groups.

2) Morphological niche breadth (MNB)

There was a wide variation on MNB among bird species and *Penelope obscura, Pipile jacutinga, Thraupis cyanoptera* and *Turdus rufiventris* had the widest MNB (One way Anova– F=6.024, df=30, $p<0.05$; Fig. 2. 3). Examining the contribution of morphological variables on PCA ordination, the traits that contributed most for this variation were the smaller diameter of the fruit, the total mass of seeds, larger and smaller diameter of the seed (Table 2. 2). The observation of MNB along the body size gradient showed that many small birds had narrow MNB (*Ilicura militaris, Euphonia pectoralis* and *Trichothraupis melanops*) and large birds had wide MNB (*Pipile jacutinga, Ramphastos dicolorus* and *Baillonius bailloni*), but much of the

MNB were not associated to the body size gradient (*Tangara cyanocephala, Tachyphonus coronatus* and *Columba plumbea*) (Appendix 2. 1).

3) Nutritional niche breadth (NNB)

Contrary to the MNB, bird species had the same range of variation in the NNB (One way Anova, F=0.811, df=30, p=0.752; Fig. 2. 4). The nutritional traits that influenced most on these variations were % sugar (soluble and insoluble) and % of protein, according to the contribution of these variables in PCA ordination (Table 2. 3). When NNB was compared along the body size gradient, there was apparently no association between then (Appendix 2. 1).

CORRELATION AMONG BIRD SPECIES AND FRUIT TRAITS

1) Description of overall patterns of correlations

Morphological traits of fruits

The first three axes had a total 3.15 of inertia and explained 23.0% of the total variance (Fig. 2. 5, Appendix 2. 2). The diameter and mass of seeds were associated with positive scores on the first ordination axis, but there was a nonsignicant ordination (Monte Carlo permutation test, 100 run, p=0.17) and explained 9.6% of the variation in the species occurrence data. The second and the third canonical axes explained better the ordination than the first axis and were positively associated with the variation in the mass of fruit and pulp. The ordination was significant on the second (Monte Carlo permutation test, p=0.02) and slight significant on the third axes (Monte Carlo permutation test, p=0.07).

Examination of bird species scores along the CCA axes indicates that the first axis divided Ramphastidae, Cotingidae and Muscicapidae with positive scores from Emberizidae and Pipridae with negatives scores and were mainly correlated with the diameter and mass of seed (Fig. 2. 5). In the second and third axis, the variation within bird families were higher than between families. Then the species distribution and aggregation did not reflect their taxonomic proximity on these axes. The second axis defined only Muscicapidae with negative scores and Tyrannidae with positive scores that were correlated with total fruit mass and pulp mass.

In relation to body mass of bird species, the first axis divided the huge and large species with positive scores and medium and small ones with negative scores, but there was not a clear body size gradient of the species scores on this axis (Fig. 2. 5), because many huge, birds like *Pipile jacutinga* were close to small birds, some small birds, like *Tangara seledon,* were close to larger birds (Appendix 2. 1).

Nutritional composition of the pulp

The first three axes had a total 2.74 of inertia and explained 20.5% of the total variance (Monte Carlo permutation test, 100 run, first axis p=0.08, second axis p=0.42, third axis p=0.42) (Fig. 2. 6, Appendix 2. 3). The first axis accounted for 11.1% of the variance and was negatively associated with % of lipid and positively with % of soluble sugar. The second canonical axis is primarily associated negatively with the variation in the % insoluble sugar and the third axis with % soluble sugar and protein.

Examination of bird species scores along the CCA axes indicated that Emberizidae and Pipridae were concentrated in the right part of the first axis with positive scores, showing their relationship with fruit with high % soluble sugar (Fig. 2. 6). In opposition, Muscicapidae, Cracidae and Tyrannidae were distributed on the left part of first axis and were correlated with fruits with high % of lipid. Ramphastidae were distributed near the origin of the CCA ordination and were defined by intermediate characteristics nutritional contents with regard to the variation within bird families, Cotingidae had the highest variation.

When the body mass of species was considered, large and medium birds had quite opposite distributions along the first axis (Fig. 2. 6, Appendix 2. 1). The large birds were correlated with high % lipid and medium ones with high % soluble sugar. Huge birds were distributed close to the origin of CCA ordination.

2) Specific correlation among niche breadth and biometric bird data.

The regression among all the dimensions of niche breadth (species richness, morphological and nutritional composition of fruit) and the biometric data of bird species showed no relations between these variables (Table 2. 4 and Appendix 2. 1).

3) Specific correlation between species richness, morphological and nutritional niche breadth.

These niche dimensions were not correlated with each other (Spearman ranking correlation - SR x MNB r=0.197, t=1.085, p=0.287; SR x NNB r=0.203, t=1.115, p=0.273; MNB x NNB r=0.285, t=1.600, p=0.1206) and the bird species did not show the similar patterns in relation to these niche dimensions. Some of them overlapped on one dimension but were separated on another.

DEFINITION OF FEEDING STRATEGIES

There were different feeding strategies for the frugivorous birds in relation to morphological (MNB) and nutritional (NNB) niche breadth and diet species richness (SR). For simultaneous analyses of these three niche dimensions, we transformed the values of niche breadth by relativization by maximum values of niche breadth and classified the values in two categories: narrow (0 – 0.50) and wide (0.51 – 1.00) for niche breadth; and low (0 – 0.50) and high (0.51 – 1.00) for diet species richness. Here, we apply the term "specialist" and "generalist" according to these categories: a bird species is considered generalist if it present a wide niche breadth or high fruit species richness in the diet. In this way, the bird species presented the following combination (Fig. 2. 7 and 2. 8):

1. **Diet generalists with high fruit species richness, nutritional flexibility and morphological specialization** - High SR, narrow MNB and wide NNB – Most of the bird species showed this feeding strategy (19sp, 61.29%). In this case, the birds restricted their tolerance in relation to morphological characteristics of fruits. The main morphological variables that influenced fruit selection were diameter and mass of the seeds and the mass of the pulp. Along the variation gradient of these variables, birds showed distinct preferences that could be summarized in four possibilities: (1) some species selected mainly fruits with small seeds and with high quantity of pulp (*Chiroxiphia caudata, Euphonia pectoralis, Habia rubica, Stephanophorus diadematus, Tangara cyanocephala, Tangara desmaresti, Trichothraupis melanops and Schiffornis virescens*) (2) small seeds with low quantity of pulp (*Ilicura militaris, Mionectes rufiventris* and *Thraupis ornata*), (3) large seeds with high quantity of pulp (*Cacicus haemorrhous, Lipaugus laniodes, Platycichla flavipes, Selenidera maculirostris* and *Turdus albicollis*), and (4) large seeds with low quantity of pulp (*Carpornis cucullatus, Myiodynastes maculatus,* and *Ramphastos dicolurus*).

2. **Diet generalists with high fruit species richness but with morphological and nutritional specialization** - High SR, narrow MNB and narrow NNB – This feeding behavior was seen only in *Columba plumbea*. This specie selected mainly fruits with small seeds with low quantity of pulp and high % soluble sugar and lipid.

3. **Diet generalists for all niche dimensions**- High SR, wide MNB and wide NNB – *Penelope obscura, Pipile jacutinga, Turdus rufiventris, Tityra cayana, Baillonius bailloni, Thraupis cyanoptera* and *Tachyphonus coronatus.* These species consumed many fruit species with large variation in morphological and nutritional aspects.

4. **Diet specialists for all niche dimensions -** Low SR, narrow MNB and narrow NNB. These species consumed few fruit species with morphological and nutritional restriction. The distribution of these species on the CCA graphics of morphology and nutritional composition showed that each species presented different criteria of selection. *Orchesticus abeillei* consumed fruits with small seeds, low quantity of pulp and rich in lipid and soluble sugar. *Orthogonys chloricterus* consumed fruits with small seeds, high quantity of pulp and rich in protein and insoluble sugar and *Tangara seledon* large seeds with high quantity of pulp rich in protein and insoluble sugar.

5. **Diet specialist on few plant species with morphological specialization and wide flexibility of nutritional composition-** Low SR, narrow MNB and wide NNB. This feeding strategy was only found in *Cissopis leveriana* that concentrated on few plant species that were morphologically similar. They chose mainly fruits with small seeds with high quantity of pulp.

DISCUSSION

1) Influence of bird body size on morphological fruit selection

According to the bird species scores on CCA ordination, fruit choice was influenced by bird body size. The general pattern was that larger birds selected fruits with larger seed mass and size and while the smaller birds selected fruits with small seeds mass and size. Body size however, was not clearly correlated with the fruit characteristics, since the species scores were not distributed on the multidimensional ordination forming a body size gradient. This pattern probably occurred because (1) other fruit characteristics, like nutritional composition, also help to determine fruit selection by frugivorous birds or (2) a biased sample of some frugivorous species.

Although fruit size can be considered the key component of fruit selection by birds because the gape width sets a rigid upper limit to the food that can be grasped and swallowed (Wheelwright 1985, Jordano 1992), here this variable alone did not exert a strong influence in the ordination of bird species in the CCA. Rather, other fruit attributes better showed their contribution in fruit selection, mainly those related to seed mass and size.

The smaller fruit dimension better described the selection than the larger one, because when the second dimension was combined with the first one both defined the shape of the fruit. In this way, elongated fruits can be swallowed more easily than spherical fruits of equal volume, due to bird morphological constraints on swallowing large fruits (Mazer and Wheelwright 1993).

The morphological niche breadth is only one dimension in the *n*-dimensional hypervolume model related with food selection; other dimensions (nutritional composition and fruit species richness in the diet) were analyzed here and showed their influence in this selection. A single niche dimension is insufficient to explain the variability found in the fruit selection by birds, resulting in a lack of relationship between bird morphology (body mass and bill size) and each dimension of the niche breadth (morphology, nutritional composition and fruit species richness). This lack of relationship was also affected by the lack of correlation between the niche breadths and because the bird species did not have the same requirements in the niche dimensions studied. For example, the niches of *Orchesticus abeillei* and *Orthogonys chloricterus* overlap and are almost identical with regard to the dimension of seed, but are distinct regarding the quantity and nutritional quality of the pulp. This feeding specialization among the consumers is important to reduce the potential trophic competition among then (Gautier-Hion *et al.* 1985, Fleming *et al.* 1987).

2) Influence of bird body mass and bill size on the range size and species diversity of fruit consumed.

Usually large animals or large-billed birds are expected to take more diverse food items within wide range size (Willson 1971, Churchfield *et al.* 1999). Our data were like some studies (Kear 1962, Newton 1967) that do not support this expectation. There was no relation between morphological niche breadth and body mass or bill dimensions in birds. The same being true for species richness of fruits consumed. Although this expected relation has been found in some sets of large and generalist frugivorous birds, like *Penelope obscura, Pipile jacutinga, Baillonius bailloni* and *Tityra cayana* (Galetti *et al.* 1997, Galetti *et al.* 2000), in this study, the lack of relation between those attributes can be explained by the highly diversified fruit diet and feeding behavior of the small and medium sized birds, that very often are capable of overcoming constraints imposed by fruit size or gape width. This is the case, for instance, of *Thraupis cyanoptera* and *Tachyphonus coronatus* (Emberizidae), medium sized birds that selected fruits within a wide morphological niche breadth from several plant species, in a very similar pattern for *Selenidera maculirostris,* a large-sized counterpart. The ability to take pieces of large fruits (e.g. Cecropiaceae, Myrtaceae and Moraceae) increases the range size of exploitable food items, which are, usually, swallowed whole by larger birds (Debussche and Isenmann 1989). The technique employed in taking small pieces of fruits, however, may require more handling time and energy expenditure than gulping fruits whole (Levey 1987, Fuentes 1994). As a consequence, although they had a wide morphological niche breadth, most of fruits sampled were from smaller fruits.

The high number of plant species consumed by birds in this study resulted not only from the diet of generalist species, but also from specialist birds. Some sets of huge and large species (*Carpornis cucullatus, Lipaugus laniodes, Selenidera maculirostris* and *Ramphastos dicolurus*) chose only fruits with large seeds. This pattern in frugivory are likely to occur in habitats with high abundance and diversity of food. A low fruit supply would force larger birds to forage on small sized-fruits, increasing their morphological niche breadth and favoring a more generalist strategy (Schoener 1991, Galetti *et al.* 2000). Evidence for decreased selectivity under conditions of low food abundance or availability has been found in many studies (McKnight and Hepp 1998, Renton 2001). The abundance and the high diversity of fruiting species in tropical forests have probably lead to bird specialization based on restrict food requirements and with low flexibility on fruit selection (Pyke *et al.* 1977).

The notion that small birds consume fruits nonselectively as they are encountered indiscriminately (generalist) (Moermond and Denslow 1985) was not supported by the present study. When birds with similar fruit species richness in the diet and different body mass were compared, we found many small birds (e.g. *Ilicura militaris* and *Euphonia pectoralis*) with narrower morphological niche breadth than the larger ones (e.g. *Platycicla flavipes* and *Lipaugus lanioides*). Furthermore, among small birds different criteria of fruit selection decreased the diet overlap and increased the exploitation of food eaten. For example, *Euphonia pectoralis* and *Ilicura militaris* selected fruits with small seeds, mainly of Melastomataceae species, but *Euphonia* consumed other fruit species with similar seed size and pulp mass, like the Cactaceae, Araceae and Bromeliaceae. *Ilicura*, on the other hand, showed more morphological flexibility and consumed other fruit species with larger and fewer seeds and low quantity of pulp, like the species of Loranthaceae and Myrsinaceae.

3) Influence of fruit nutrients on fruit choice by birds

In contrast with the high morphological specialization found in most birds, the general pattern observed for nutritional niche breadth is a generalist feeding strategy. This result is similar to that reported by other authors (Whelan and Willson 1994, Galetti *et al.* 2000) and seems to suggest that the strong nutritional imbalance characterizing the pulp of most fruit species should force frugivores to have mixed-species diets with high variation on nutritional content in order to get a balanced input of energy, protein, vitamins, and minerals (Herrera 1985). The bird species showed a wide flexibility concerning the nutritional fruit traits but not with the same nutritional requirement. According to the position of bird species on the CCA graphic, some birds families showed similar requirements. For example, Muscicapidae and Tyrannidae chose mainly lipid-rich fruit and Emberizidae and Pipridae sugar-rich fruit. Other authors observed these same preferences also (Moermond and Denslow 1985, Witmer and Van Soest 1998, Witmer 1999, Bouen and Ornelas 2001) which should reflect their nutritional requirements and their physiological and biochemical restrictions (Karasov and Levey 1990, Witmer and Van Soest 1998, Levey *et al.* 1999). According to Fuentes (1994), lipid-rich fruits are selected by bird species with slower food passage rates through the digestive tract. These birds also feed frequently on insects. Bird species with faster food passage rates eat less insects and more fruits rich in sugar and water. Lipids probably need more time to be assimilated than simple sugars, as they must be hydrolyzed and emulsified before being transported through the intestine walls.

Although large birds ingested predominantly lipid-rich fruits and the medium birds preferred sugar-rich fruits, our results do not support the idea of correlation between nutrition content and frugivorous body mass (Leighton and Leighton 1983). The same results was found by Witmer and Soest (1998).

4) Ecological implications of frugivore nutrition and evolution of plant/frugivore mutualisms

The association between high quality fruits and large specialized fruit-eating birds (*sensu* Snow, 1981) was not verified here because many omnivores and frugivores/insectivores (e.g. *Turdus rufiventris, Myiodynastes maculates* and *Mionectes rufiventris*) selected fruits with more concentration of lipids than the larger frugivores (e.g. *Carpornis cucullatus, Ramphatos dicolorus,* B*aillonius bailloni* and *Penelope obscura*). Similar results were also found by other authors (Buen and Ornelas 2001, Galetti *et al.* 1997). In Europe, the bird species that show stronger preference for most lipid-rich fruits were only moderately frugivorous, and some were also very poor dispersers (Traveset 1993). Several authors had previously argued that we should not expect correlations between seed-dispersing efficiency of birds and their patterns of fruit choice or dependence on fruits (Wheelwright and Orians 1982, Davidar 1987, Levey 1987). Furthermore, the relatively high energy density of lipids are not necessarily nutritionally superior to sugary fruits (Witmer and Van Soest 1998). Relative consumption of lipids and sugar depends not only on digestive specialization of a particular species, but also on nutritional needs. Glucose is an essential fuel for the brain and other tissues, and animals cannot biochemically manufacture glucose from fatty acids. The roles of simple sugars and lipids as essential fuels and energy depots, respectively, are likely to influence fruit selection (Witmer and Van Soest 1998). These results clearly indicates that the proposed association between large specialist birds and lipid-rich fruits and, consequently, the evolutionary ideas about plant/frugivore mutualisms (Mckey 1975, Stiles 1993) deserve a more carefully examination (Fuentes 1994, Buen and Ornelas 2001).

CONCLUSION

In general, birds eat a high diversity of fruit species; but at the same time, they show clear preference and select fruits according to morphological and nutritional traits and with high species richness. The fruit morphological specialization was associated with bird size. The larger birds selected fruits with larger seed mass and size and while the smaller birds selected fruits with small seeds mass and size. In contrast with the high morphological specialization, the general pattern observed for nutritional composition is a generalist feeding strategy. It seems to suggest that the strong nutritional imbalance characterizing the pulp of most fruit species should force frugivores to have mixed-species diets with high variation on nutritional content in order to get a balanced input of energy, protein, vitamins, and minerals. The bird species showed a wide flexibility concerning the nutritional fruit traits but not with the same nutritional requirement. The fruit species richness consumed by birds was not associated with bird size and neither with morphological and/or nutritional traits of fruit consumed. These results may have evolutionary implications in the plant/frugivore mutualisms.

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LITERATURE CITED

ANDERSON, M.,T. and MATHIS, A. 1999. Diets of two sympatric neotropical salamanders, *Bolitoglossa mexicana* and *B. rufescens*, with notes on reproduction for *B. rufescens*. *Journal of Herpetology* 33: 601-607.

BLAKE, G. B. and LOISELLE, B. A. 2001. Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. *Auk* 118(2): 304-326.

BLAKE, G. B. and LOISELLE, B. A. 2000. Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. *Auk* 117(3): 663-686.

BLIGH, E. G. and DYER,W. J. 1959. A rapid method of total lipid extraction and purification. *Can. J. Biochem. Physiol.* 37: 911-917.

BRANDL R., KRISTIN, A., and LEISLER, B. 1994. Dietary niche breadth in a local community of passerine birds: An analysis using phylogenetic contrasts. *Oecologia* 98(1): 109-116.

BUEN, L. L. and ORNELAS, J. F. 2001. Seed dispersal of he mistletoe *Psittacanthus schiedeanus* by birds in Central Veracruz, Mexico. *Biotropica* 33(3): 487-494.

CARNES, B. A. and SLADE, N. A. 1982. Some comments on niche analysis in canonical space. *Ecology* 63: 888-893.

CHURCHFIELD, S., NESTERENKO, V. A., and SHVARTS, E. A. 1999. Food niche overlap and ecological separation amongst six species of coexisting forest shrews (Insectivora: Soricidae) in the Russian Far East. *Journal of Zoology* 248(3): 349-359.

DAVIDAR, P. 1987. Fruit structure in two neotropical mistletoes and its consequences for seed dispersal. *Biotropica* 19: 137-139.

DEBUSSCHE, M. and ISENMANN, P. 1989. Fleshy fruit characters and the choices of bird and mammal seed dispersers in a Mediterranean Region. *Oikos* 56(3): 327-338.

FALES, F. W. 1951. The assimilation and degradation of carbohydrates by yeast cells. *J. Biol. Chem.* 193: 113-124.

FINCH, D. M. 1989. Habitat use and habitat overlap of riparian birds in three elevational zones. *Ecology* 70(4): 866-880.

FLEMING, T. H., BREITWISCH, R., and WHITESIDES, G. H. 1987. Patterns of tropical vertebrate frugivore diversity. *Ann. Rev. Ecol. Syst.* 18: 91-109.

FUENTES, M. 1994. Diets of fruit-eating birds: What are the causes of interspecific differences? *Oecologia* 97(1): 134-142.

GALETTI, M., LAPS, R., and PIZO, M. A. 2000. Frugivory by Toucans (Ramphastidae) at two altitudes in the Atlantic Forest of Brazil. *Biotropica* 32(4b): 842-850.

GALETTI, M., MARTUSCELLI, P., OLMOS, F., and ALEIXO, A. 1997. Ecology and conservation of the jacutinga *Pipile jacutinga* in the Atlantic Forest of Brazil. *Biological Conservation* 82: 31-39.

GAUTIER-HION, A., DUPLANTIER, J-M, QURIS, R., FEER, F., SOURD, C., DECOUX, J-P., DUBOST, G., EMMONS, L., ERARD, C., HECKETSWEILER, P., MOUNGAZI, A., ROUSSILHON, C., and THIOLLAY, J-M. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65(3): 324-337.

GOMES, V. S. M. 2001. *Variação espaço-temporal de aves frugívoras no sub-bosque e chuva de sementes em um trecho de Mata Atlântica no Estado de São Paulo*. MsC. Thesis, University of Campinas, São Paulo, Brazil. 82p.

GOTELLI, N. J. and ENTSMINGER., G. L. 2001. *EcoSim: Null models software for ecology.* Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsmin/ecosim.htm.

GREGORY, R. and GASTON, K. J. 2000. Explanations of commonness and rarity in British breeding birds: Separating resource use and resource availability. *Oikos*. 88(3): 515-526.

GREIG-SMITH, P. W. 1986. Bicolored fruit displays and frugivorous birds: the importance of fruit quality to dispersers and seed predators. *American Naturalist* 127(2): 246-251.

HERRERA, C. M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* 63(3): 773-785.

HERRERA, C. M. 1985. *Habitat-consumer: Interactions in frugivorous birds*. Pp. 341-365. *In*: Cody, M. L. (ed.) Habitat selection in birds (Physiological ecology). Academic Press Inc.

HERRERA, C. M. 1992. Interspecific variation in fruit shape allometry phylogeny and adaptation to dispersal agents. *Ecology*. 73(5): 1832-1841.

HOWE, H. F. 1993. Specialized and generalized dispersal systems: Where does " the paradigm" stand? *Vegetatio* 107/108: 3-13.

JEFFERY, G.H., BASSETT, J., MENDAHAM, J, and DENNEY, R.C. 1989 *Vogel's Textbook of Quantitative Chemical Analysis*. 4th edition. London, Longman Group.

JORDANO, P. 1986. Frugivory, external morphology and digestive system in Mediterranean Sylviid warblers *Sylvia* spp. *Ibis* 129: 175-189.

JORDANO, P. 1992. *Fruits and frugivory*. Pp. 105-153. *In*: Fenner, M. (ed.). Seed: The ecology of regeneration in plant communities. Oxon. CAB International.

KARASOV, W. H. and LEVEY, D. J. 1990. Digestive system trade-offs and adaptations of frugivorous passerine birds. *Physiological zoology* 63(6): 1248-1270.

KEAR, J. 1962. Food selection in finches with special reference to interspecific differences. *Proc. Zool. Soc. London*. 138: 163-201.

KEARNS, C. A and INOUYE, D. W. 1993 *Techniques for pollination biologists*. University Press of Colorado.

KREBS, C. J. 1999. *Ecological Methodology 2* ed. Addison –Wesley Educational Publishers Inc. 620 p.

LEIGHTON, M. and LEIGHTON, D. R. 1983. *Vertebrate responses to fruiting seasonality within a Bornean rain forest.* Pp. 181-196. *In:* Sutton, S. L., Whitmore, T. C. and Chadmuck, A. C. (Eds.). Tropical rain forest: Ecology and management Blackwell Sci. Publ. , London.

LEVEY, D. J. 1987. Seed and size fruit-handling techniques of avian frugivores. *American Naturalist* 129: 471-485.

LEVEY, D. J. and CIPOLLINI, M. L. 1998. A glycoalkaloid in ripe fruit deters consumption by cedar waxings. *Auk* 115(2): 359-367.

LUISELLI, L., AKANI, G. C., and CAPIZZI, D. 1998. Food resource partitioning of a community of snakes in a swamp rainforest of south-eastern Nigeria. *Journal of Zoology* 246(2): 125-133.

MANTOVANI, W. 2001 *A paisagem dinâmica.* Pp. 81-91. *In:* Leonel, C. Intervales. Fundação para a conservação e produção florestal do Estado de São Paulo. Secretaria de Estado do Meio Ambiente.

MANTOVANI, W., RODRIGUES, R. R., ROSSI, L., ROMANIUC-NETO, S., CATHARINO, E. L. M., and CORDEIRO, I. 1990. *A vegetação na Serra do Mar em Salesópolis, SP.* 1: 348-384. *In:* II Simpósio de Ecossistemas da Costa Sul e Sudeste Brasileira: estrutura, função e manejo, Academia de Ciências do Estado de São Paulo, Águas de Lindóia.

MARTIN, T. E . 1985. Resource selection by tropical frugivorous birds integrating multiple interactions. *Oecologia* 66(4): 563-573.

MAURER, B. A. 1996. *Energetics of avian foraging*. Pp. 250-279. *In*: Carey, C. (Ed.) Avian energetics nutritional ecology. ITP International Thomson Publishing.

MAZER S. J. and WHEELWRIGHT, N. T. 1993. Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants. *Evolutionary Ecology* 7(6): 556-575.

McCUNE, B., and MEFFORD, M. J. 1999. *PC-ORD for Windows. Multivariate analysis of ecological data.* Version 4.10. MjM Software, Gleneden Beach, Oregon, USA.

McKEY, D. 1975. *The ecology of coevolved seed dispersal systems*. Pp. 159-191. *In:* Gilbert, L.E. and Raven, P. H. (eds.). Coevolution of animals and plants. University of Texas Press, Austin, TX.

MCKNIGHT, S. K., and HEPP, G. R. 1998. Foraging-niche dynamics of gadwalls and American coots in winter. *Auk* 115(3): 670-683.

MOERMOND, T. C., and DENSLOW, J. S. 1985. *Neotropical avian frugivores: patterns of behaviour, morphology, and nutrition with consequences for food selection*. Pp. 865-897. *In:* Buckley, P. A.; Foster, M. S.; Morton, E. S.; Ridgely, R. S.; Smith, N. G. (Eds:). Neotropical Ornithology. Ornithological Monographs. Vol. 36.

MURPHY, M. E. 1996. *Nutrition and Metabolism*. Pp.32-60. *In:* Carey, C. (ed.). Avian energetics nutritional ecology. ITP International Thomson Publishing.

NAKANISHI, H 1996. Fruit color and fruit size of bird-disseminated plants in Japan. *Vegetatio* 123: 207-218.

NEWTON, I. 1967. The advantage radiation and feeding ecology of some British finches. *Ibis* 109: 33-98.

OLIVEIRA-FILHO, A. T. and FONTES, M. A. L. 2000. Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. *Biotropica* 32(4b): 793-810.

PIANKA, E. R. 1988. *Evolutionary ecology*. Harper & Row, Publishers, Inc. 468 p.

PIJL, L. VAN DER. 1982. *Principles of dispersal in higher plants*. 3 ed. Berlin, Springer Verlag, 215 p.

PIZO, M. A. 2002. *The seed-dispersers and fruit syndromes of Myrtaceae in the Brazilian Atlantic Forest*. Pp. 129-143. *In*: Levey, D. J.; Silva, W. R. and Galetti, M. (Eds.) Frugivory and seed dispersal: ecology, evolution and conservation. Wallingford, CABI Publishing.

POORTER, H. and VILLAR, R., 1997. "The fate acquired carbon in plants: chemical composition and construction costs". *In:* Bazzaz, F. A. and Grace, J. (Eds.) *Plant Resource and Allocation*. Academic Press.

PYKE, G. H., PULLIAM, H. R. and CHARNOV, E. L. 1977. Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* 52: 137-154.

RENTON, K. 2001. Lilac-crowned parrot diet and food resource availability: Resource tracking by a parrot seed predator. *Condor* 103(1): 62-69.

SABATES, A. and SAIZ, E. 2000. Intra- and interspecific variability in prey size and niche breadth of myctophiform fish larvae. *Marine Ecology-Progress Series* 201(9): 261-271.

SCHOENER, T. W. 1991. *Theory of feeding strategies*. Pp. 409-444. *In*: Real, L. A. and Brown, J. H. (Eds.). Foundations of ecology: Classic papers with commentaries. The University of Chicago Press.

SCHOENER, T. W. and JANZEN, D. 1968. Notes on environmental determinants of tropical versus temperate insects size patterns. *American Naturalist* 102: 207-224.

SMA 2001. *Intervales*. São Paulo: Secretaria do Estado do Meio Ambiente. 240p.

SNOW, D. W. 1981. Tropical frugivorous birds and their food plants; a would survey. *Biotropica* 13: 1-14.

STATISTICA 1993. *Statistica For Windows*. Release 4.2. Statsoft, Inc.

STILES, E. W. 1993. The influence of pulp lipids on fruit preference by birds *Vegetatio* 107/108: 227-235.

SUN, C., MOERMOND, T.C., and GIVNISH, T. 1997. Nutritional determinant of diet in three turacos in a tropical montane forest. *Auk* 114(2): 200-211.

TER BRAAK, C. J. F. 1986. Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.

TRAVESET, A. 1993. Weak interactions between avian and insect frugivores: the case of *Pistacia terebinthus* L. (Anacardiaceae). *Vegetatio* 107/108: 191-203.

VAN VALEN, L. and GRANT, P. R. 1970. Variation and niche width reexamined. *American Naturalist*. 104: 589-590.

WHEELWRIGTH, N. T. 1985. Fruit size, gape width and the diets of fruit-eating birds. *Ecology* 66: 808-818.

WHEELWRIGTH, N. T. and ORIANS, G. H. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *American Naturalist* 119: 402-413.

WHELAN, C. J. and WILLSON, M. F. 1994. Fruit choice in migrating North American birds: field and aviary experiments. *Oikos* 71: 137-151.

WILLSON, M. F. 1971. Seed selection in some North American Finches. *Condor* 73: 415-429.

WITMER, M. C. 1999. Do avian frugivores absorb fruit sugars inefficiently? How dietary nutrient concentration can affect coefficients of digestive efficiency. *Journal of Avian Biology* 30(2): 159-164.

WITMER, M. C. and VAN SOEST, P. J. 1998. Contrasting digestive strategies of fruit-eating birds. *Functional Ecology* 12(5): 728-741.

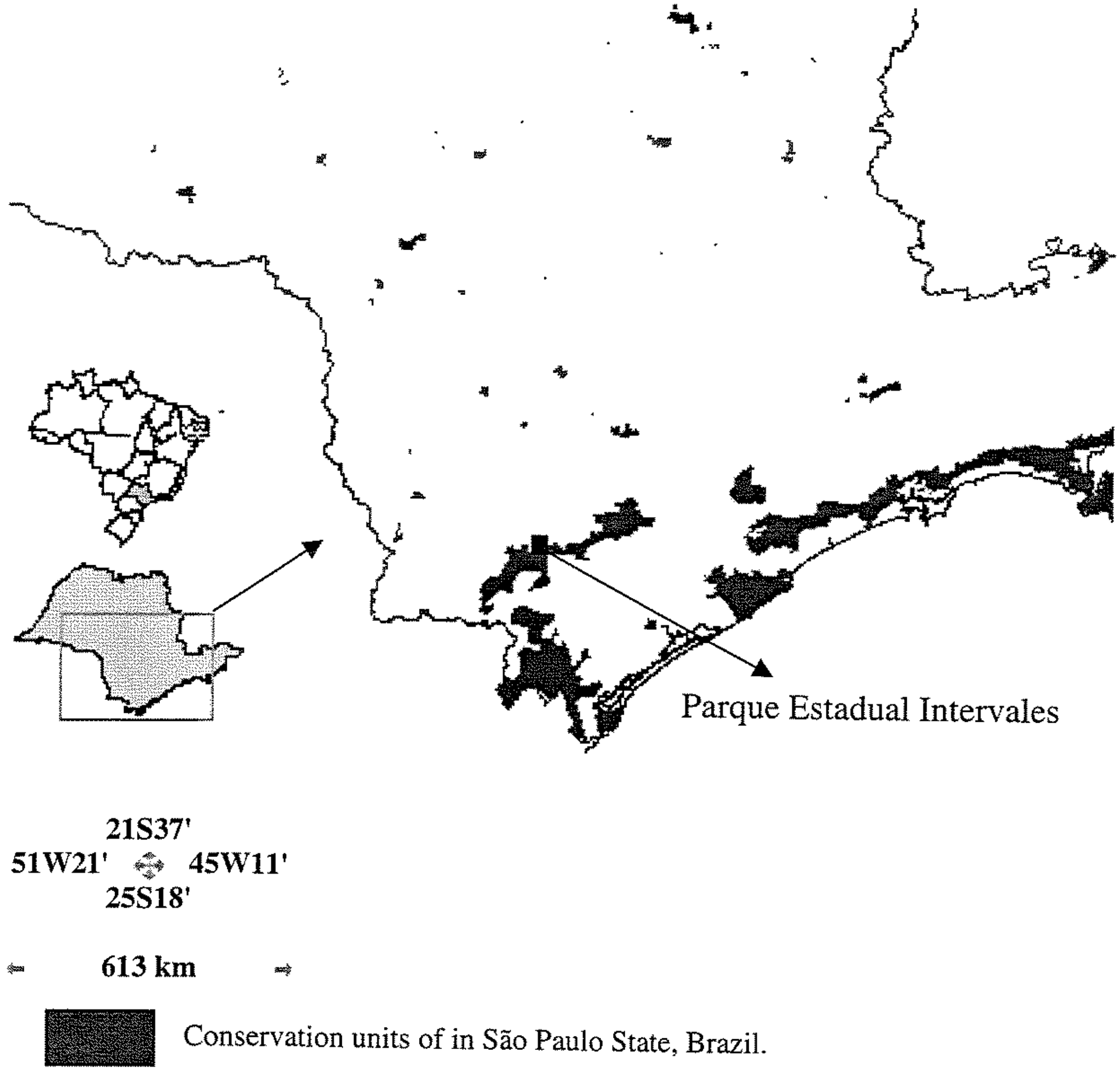

Fig. 2. 1. Localization of Parque Estadual Intervales in southern São Paulo State.

ble 2. 1. Mean fruit species richness and 95% CI for number of plant species expected in 15, 20 and 30 mples in the diet of 31 bird species, based on 100 simulations. The bird species were classified in four oups according their mean richness of plant species consumed. Means are considered different if CIs do t overlap.

		15 samples			20 samples			30 samples		
roup	Bird	Mean Richness	CI.Low	CI.High	Mean Richness	CI.Low	CI.High	Mean Richness	CI.Low	CI.Hig
1	Cislev	4.98	4.70	5.26						
1	Tansel	5.44	4.19	6.68	5.81	5.04	6.59			
1	Ortchl	5.59	4.08	7.10	6.00	4.57	7.42	6.61	5.54	7.67
1	Orcabe	5.95	4.38	7.52	6.55	5.40	7.70			
1	Pipjac	6.51	5.34	7.67						
1	Liplan	6.80	4.64	8.96	7.85	5.75	9.94	9.32	7.90	10.74
2	Tandes	7.27	4.79	9.74	8.55	5.96	11.15	10.54	8.01	13.07
2	Cachae	7.82	4.93	10.72	9.23	6.05	12.40	11.49	8.07	14.90
2	Throrn	8.11	5.93	10.29	9.38	7.30	11.47	11.04	9.48	12.61
2	Titcay	8.30	6.22	10.37	9.42	7.57	11.28	11.00	11.00	11.00
2	Plafla	8.32	5.64	11.00	10.26	7.65	12.87	13.54	11.73	15.35
2	Myimac	8.41	7.16	9.65						
2	Tancya	8.67	6.57	10.77	9.80	7.79	11.82	11.20	9.68	12.72
2	Ramdic	8.69	7.78	9.60						
2	Colplum	9.00	9.00	9.00						
3	Selmac	9.94	7.85	12.03	11.78	10.10	13.46			
3	Stedia	10.00	10.00	10.00						
3	Habrub	10.07	8.26	11.89	12.00	12.00	12.00			
3	Taccor	10.09	8.14	12.03	11.91	10.32	13.49			
3	Baibail	10.15	7.79	12.51	11.99	9.52	14.45	14.58	12.68	16.47
3	Trimel	10.23	7.42	13.03	12.34	9.03	15.65	15.69	11.96	19.42
3	Carcuc	10.23	7.34	13.12	12.51	9.37	15.64	16.47	13.24	19.69
3	Turalb	10.29	7.13	13.44	12.78	9.45	16.12	17.31	13.69	20.94
3	Schvir	10.45	8.49	12.40	12.62	11.67	13.57			
3	Thrcya	10.57	7.94	13.21	12.84	9.94	15.75	16.43	13.39	19.47
4	Euppec	11.15	8.64	13.66	13.82	11.27	16.36	18.20	16.30	20.10
4	Turruf	11.17	8.68	13.65	13.78	11.13	16.44	18.09	16.15	20.03
4	Chicau	11.67	8.81	14.53	14.53	11.31	17.75	19.42	15.62	23.22
4	Mioruf	11.70	9.42	13.98	14.62	12.51	16.72			
4	Penobs	11.81	9.44	14.18	14.81	12.35	17.26	20.05	18.71	21.39
4	Ilimil	11.89	10.06	13.72	14.57	13.59	15.54			

Species composition of groups as in Fig. 2. 2 footnote.

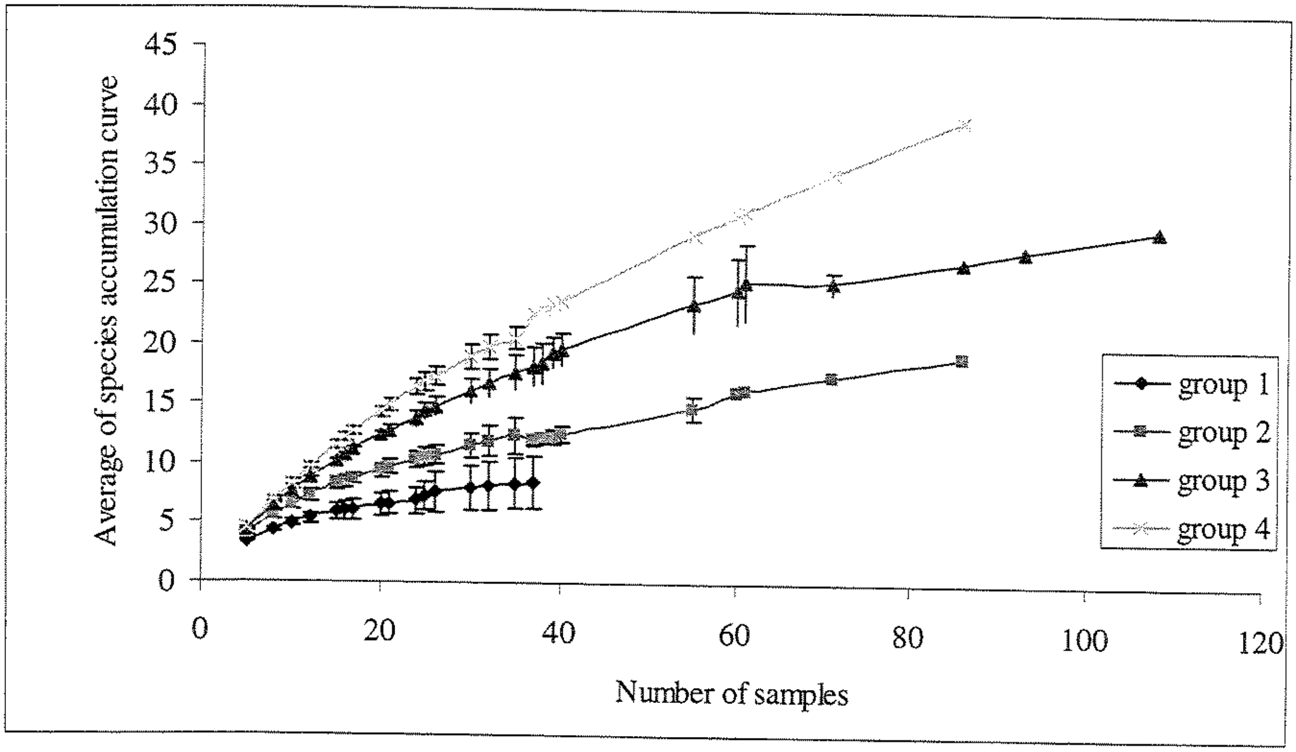

Fig. 2. 2. Average of plant species accumulation curve for each bird group. These groups comprised 31 bird species and were classified according to the species richness mean of plant consumed.

Species abbreviations:

Group 1: *Cissopis leveriana* (Cislev), *Tangara seledon* (Tansel), *Orthogonys chloricterus* (Ortchl), *Orchesticus abeillei* (Orcabe), *Pipile jacutinga* (Pipjac), *Lipaugus lanioides* (Liplan).

Group 2: *Tangara desmaresti* (Tandes), *Cacicus haemorrhous* (Cachae), *Thraupis ornata* (Throrn), *Tityra cayana* (Titcay), *Platycichla flavipes* (Plafla), *Myiodynastes maculatus* (Myimac), *Tangara cyanocephala* (Tancya), *Ramphastos dicolorus* (Ramdic) *Columba plumbea* (Colplum).

Group 3: *Selenidera maculirostris* (Selmac), *Stephanophorus diadematus* (Stedia), *Habia rubica* (Habrub), *Tachyphonus coronatus* (Taccor), *Baillonius bailloni* (Baibail), *Trichothraupis melanops* (Trimel), *Carpornis cucullatus* (Carcuc), *Turdus albicollis* (Turalb), *Schiffornis virescens* (Schvir), *Thraupis cyanoptera* (Thrcya).

Group 4: *Euphonia pectoralis* (Euppec), *Turdus rufiventris* (Turruf), *Chiroxiphia caudata* (Chicau), *Mionectes rufiventris* (Mioruf), *Penelope obscura* (Penobs), *Ilicura militaris* (Ilimil).

Table 2. 2. Results of a PCA conducted on nine morphological traits of fruits of 132 plants species eaten by 31 bird species.

	First six envectors					
	1	2	3	4	5	6
Eigenvalue	3.96	2.56	1.60	0.39	0.27	0.16
% of variance	44.0	28.4	17.8	4.4	3.0	1.8
Cum% of variance	44.0	72.4	90.2	94.5	97.5	99.3
Total fruit mass	-0.38	-0.26	-0.38	0.00	0.03	0.35
Total seeds mass	-0.40	-0.13	0.39	-0.36	0.22	0.13
Pulp mass	-0.36	-0.26	-0.43	0.03	0.01	0.35
Larger fruit diameter	-0.37	-0.22	0.40	-0.43	-0.09	-0.27
Smaller fruit diameter	-0.43	-0.04	-0.30	0.28	-0.08	-0.77
Number of seeds	-0.15	-0.32	0.52	0.73	-0.20	0.18
One seed mass	-0.27	0.45	0.10	0.26	0.76	0.03
Larger seed diameter	-0.26	0.50	0.05	-0.02	-0.45	0.19
Smaller seed diameter	-0.27	0.50	0.02	0.00	-0.33	0.11

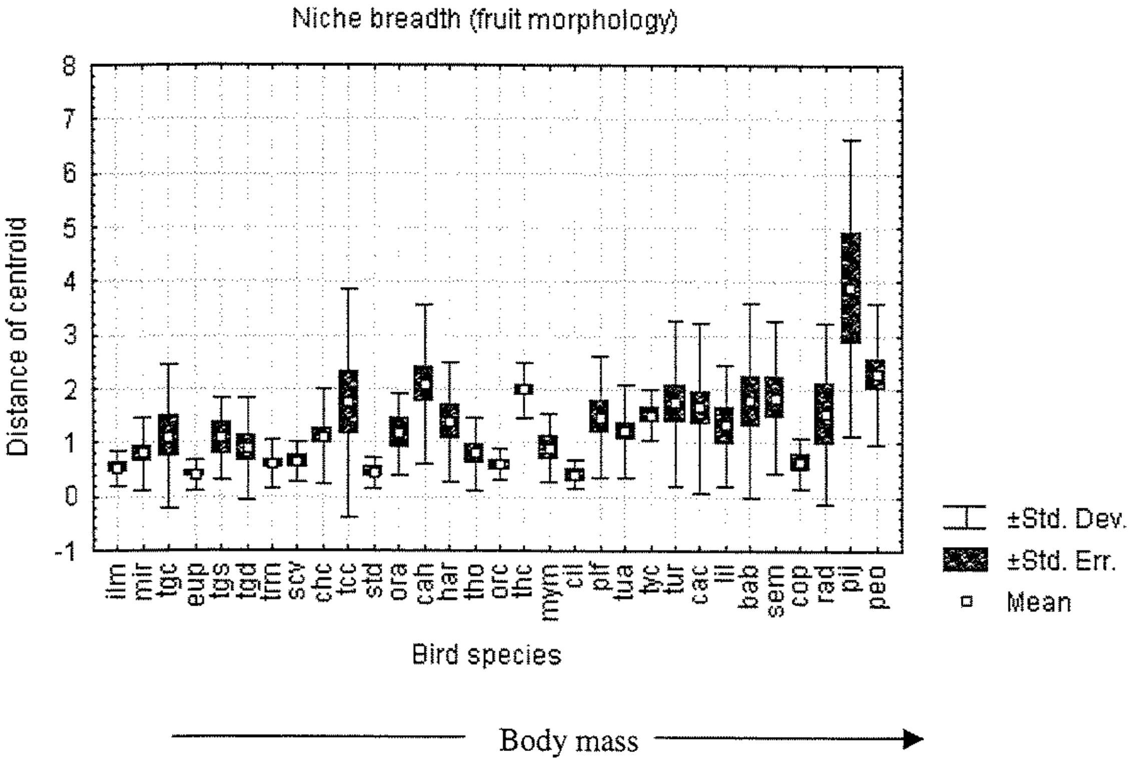

Fig. 2. 3. Measure of the morphological niche breadth of 31 bird species defined by the Std. Dev. of plant species scores distance from centroid on PCA. The bird species were distributed on box-plot in body mass gradient. Species abbreviations consisted of the first two letters of the genus and first one letter of the species epithet: see Appendix 2. 1

Table 2. 3. Results of a PCA conducted on four nutritional composition traits of fruits of 117 plants species eaten by 31 bird species.

	First four Eigenvectors			
	1	2	3	4
Eigenvalue	1.92	1.00	0.66	0.43
%variance	47.9	24.9	16.5	10.7
Cum.%variance	47.9	72.8	89.3	100.0
% protein	0.26	0.87	-0.42	0.02
%lipid	0.45	-0.50	-0.74	-0.04
% soluble sugar	-0.60	-0.02	-0.39	0.70
% insoluble sugar	-0.60	0.03	-0.35	-0.72

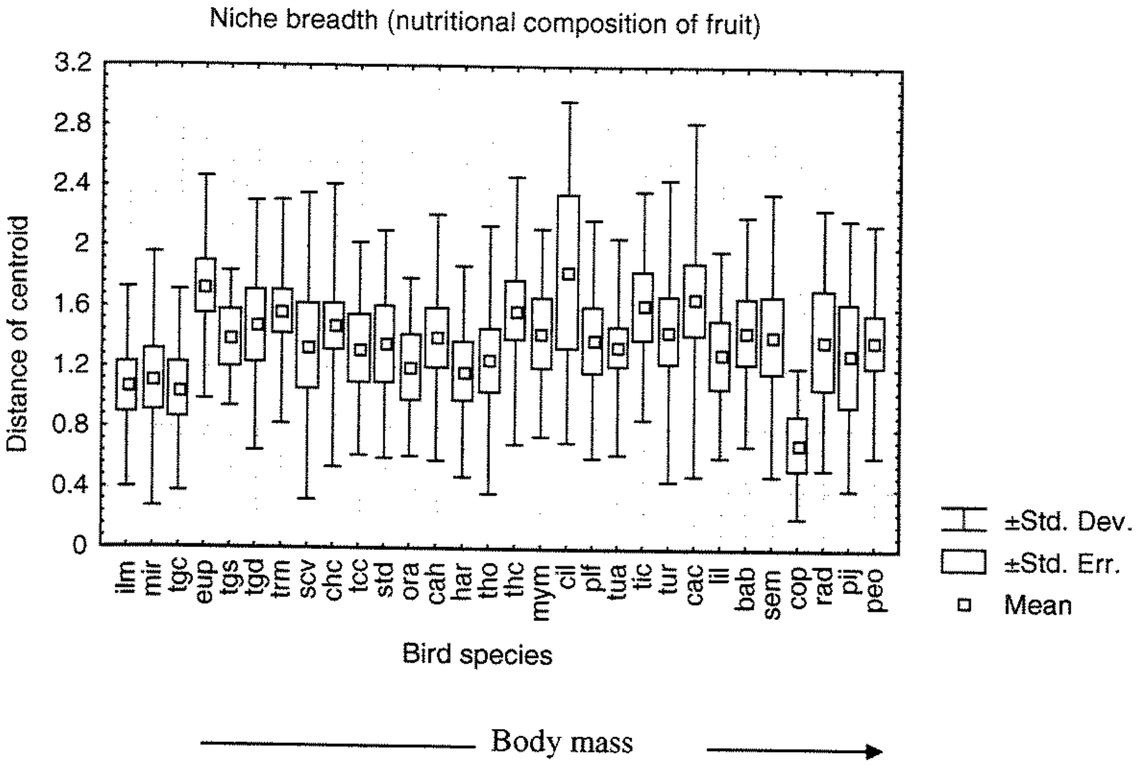

Fig. 2. 4. Measure of the nutritional niche breadth of 31 bird species defined by the Std. Dev. of plant species scores distance from centroid on PCA. The bird species were distributed on box-plot in body mass gradient. Species abbreviations consisted of the first two letters of the genus and first one letter of the species epithet: see Appendix 2. 1.

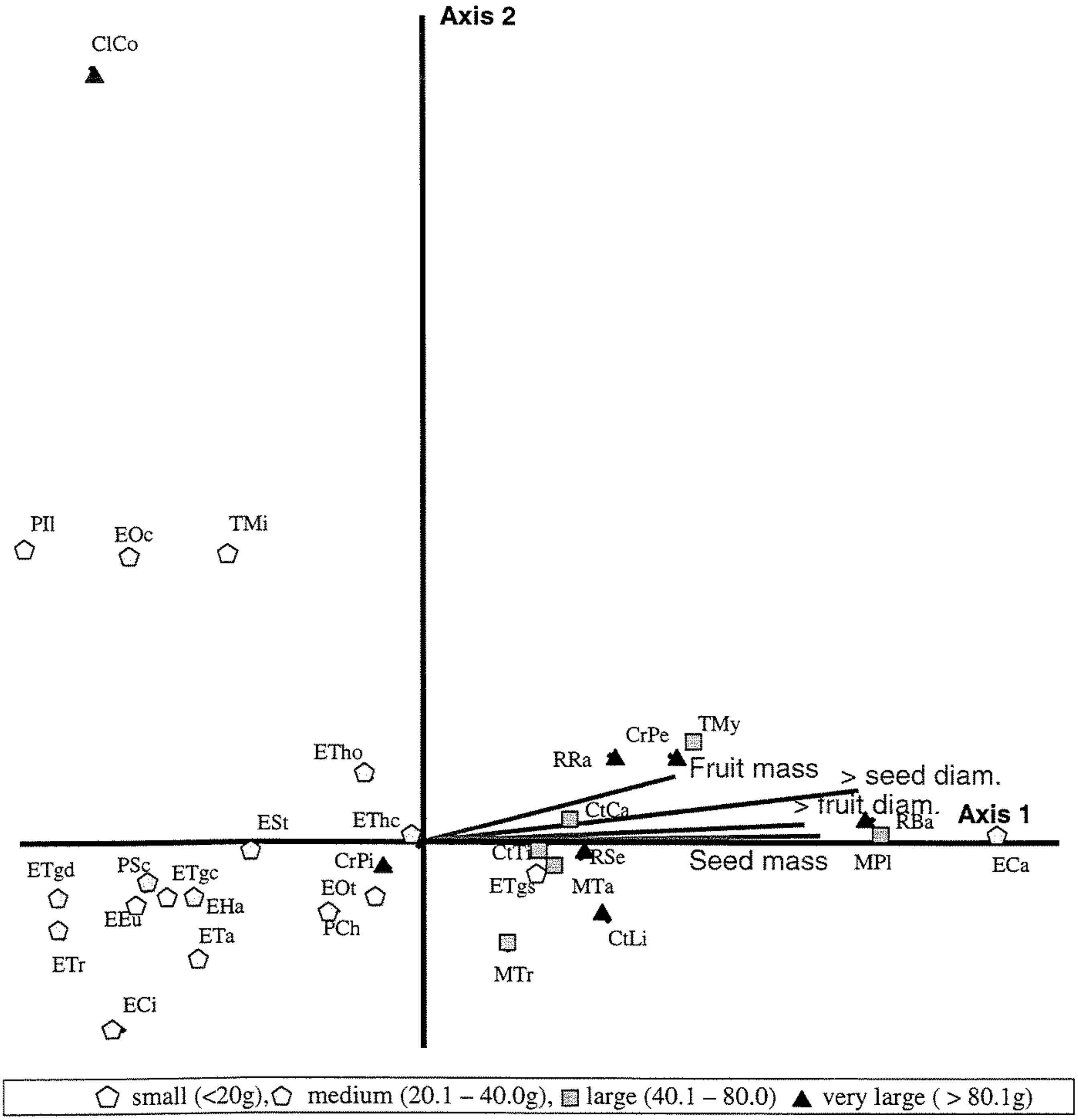

Fig. 2. 5. Position of 31 bird species in the biplot of canonical correspondence analyses (CCA) for axis 1 and 2 where six morphological variables of fruits of 41 plant families (mass of fruit, seed and pulp, diameter of fruit and seed and number of seeds) were correlated. Bird species were denoted with the first letter of the family and the first two letters of the genus, in case of families of the same first letter, we added one more letter, and we also did the same for species of the same genus. Four categories were defined for bird mass: small (<20g), medium (20.1 – 40.0g), large (40.1 – 80.0) and very large (> 80.1g) (see Appendix 2. 1). For a detailed comprehension of statistical results see appendix 2. 2.

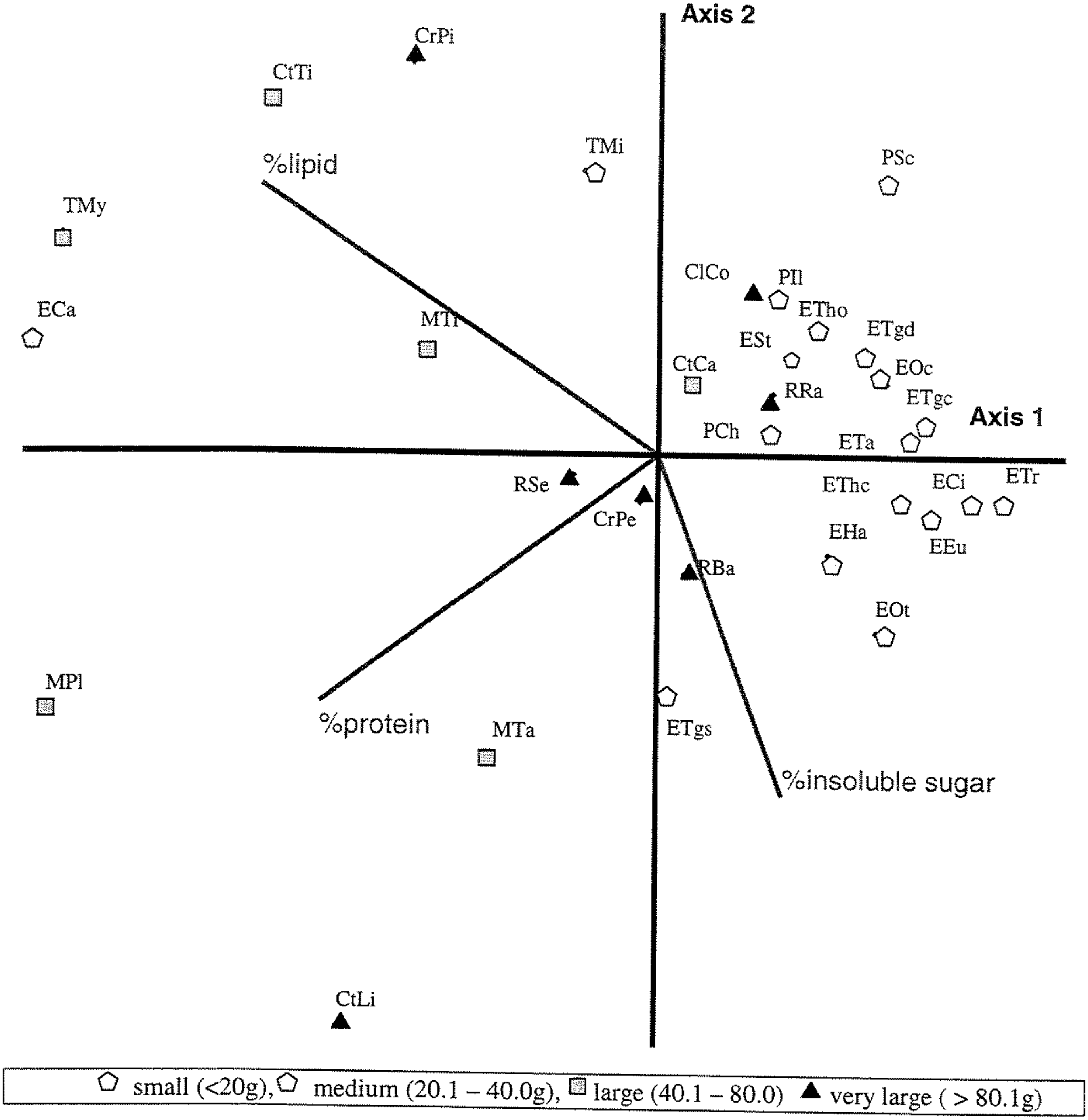

Fig. 2. 6. Position of 31 bird species in the biplot of canonical correspondence analyses (CCA) for axis 1 and 2 where four morphological variables (% protein, lipid, soluble sugar and insoluble sugar) of fruits of 29 plant families were correlated. Bird species were denoted with the first letter of the family and the first two letters of the genus, in case of families of the same first letter, we added one more letter, and we also did the same for species of the same genus. Four categories were defined for bird mass: small (<20g), medium (20.1 – 40.0g), large (40.1 – 80.0) and very large (> 80.1g) (see Appendix 2. 1). For a detailed comprehension of statistical results see appendix 2. 3.

Table 2. 4. Multiple linear regression among niche breadth (fruit morphology, nutritional composition and species richness) and bird morphology.

Multiple linear regression - Dependent variables: median of body mass and bill dimensions (length, width and depth)				
Niche breadth	**R²**	**BETA**	**T (23)**	**p**
Fruit morphology	0.12	0.20	0.92	0.367
Nutritional composition	0.30	0.02	0.10	0.920
Avarege species richness (15 samples)	0.24	-0.14	-0.60	0.556

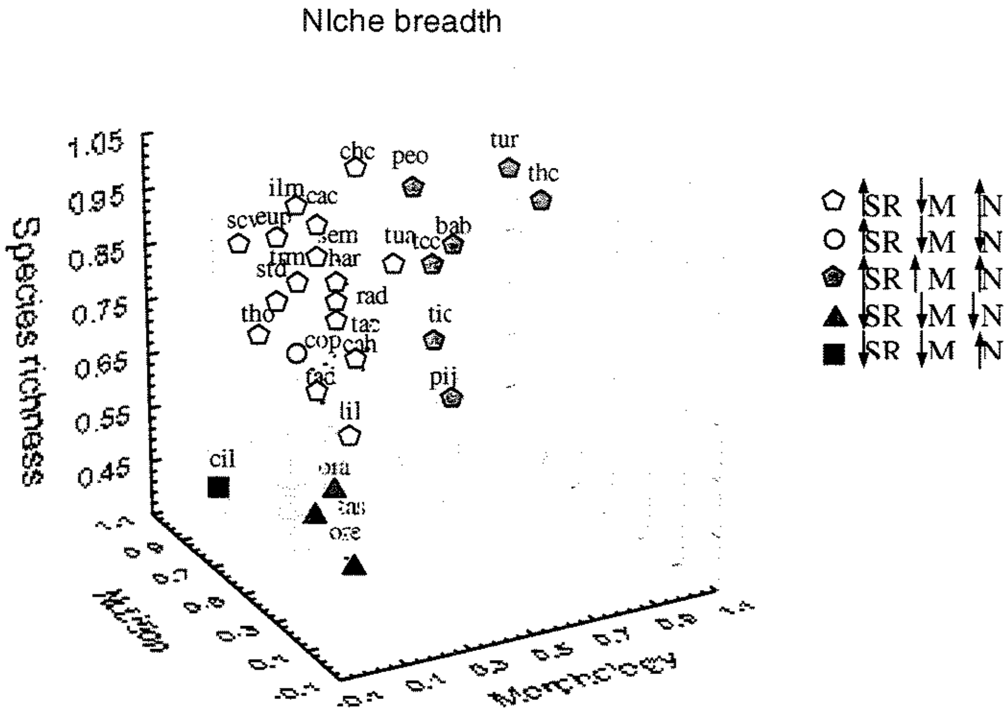

Fig.2. 7 Three dimension diagram of feeding strategies of 31 frugivorous birds in relation to morphological (M) and nutritional (N) niche breadth and diet species richness (SR). The values of niche breadth were relativizated by maximum values of niche breadth for simultaneous analyses of these three niche dimensions and the frugivorous birds were classified by these values. Species abbreviations consisted of the first two letters of the genus and first one letter of the species epithet: see Appendix 2. 1.

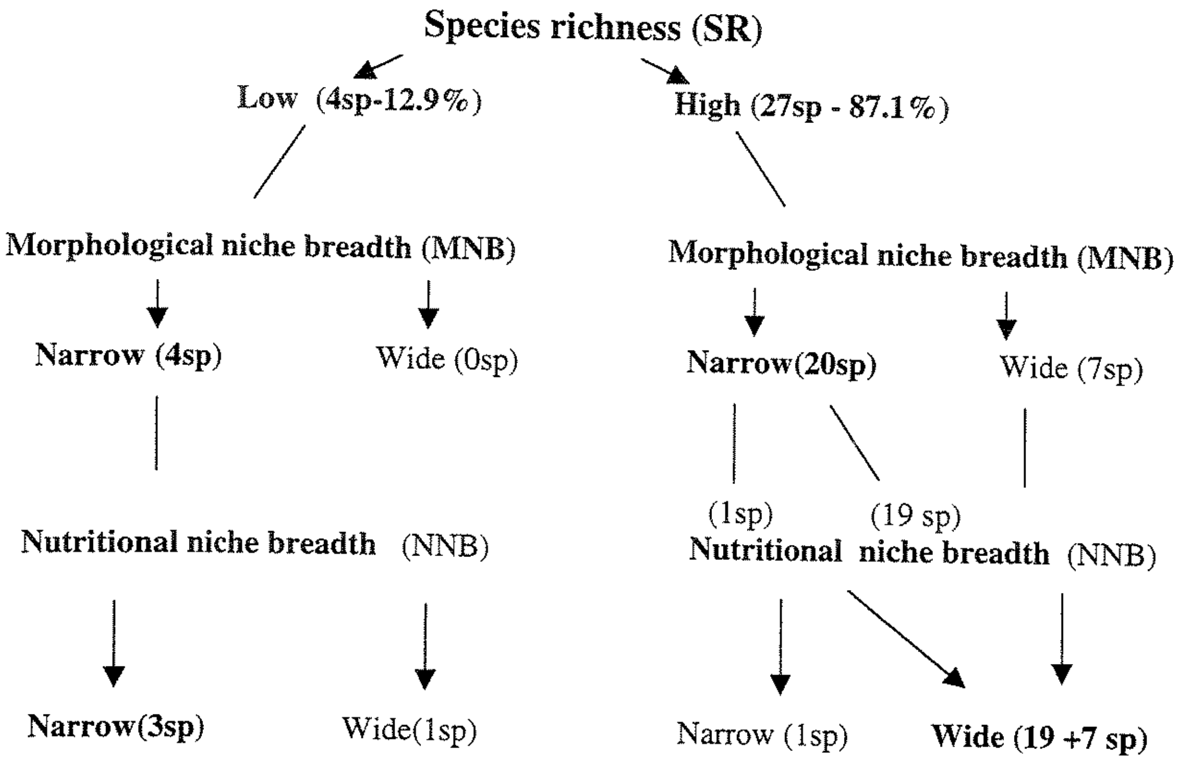

Fig. 2. 8. Schematic representation of the possible feeding strategies of 31 frugivorous birds in relation to morphological (MNB) and nutritional (NNB) and diet species richness (SR).

Appendix 2. 1. List of bird species and the median of their morphological data captured in Parque Estadual Intervales in southern São Paulo State.

Family	**Species**	**N.**	**Body mass (g)**	**Bill length (cm)**	**Bill width (cm)**	**Bill depth (cm)**
Cracidae	*Penelope obscura*	0	-	-	-	-
Cracidae	*Pipile jacutinga*	1	1200.0	-	-	-
Columbidae	*Columba plumbea*	1	231.0	1.49	0.60	0.50
Ramphastidae	*Baillonius bailloni*	3	137.0	5.01	2.23	2.25
Ramphastidae	*Ramphastos dicolorus*	7	291.0	9.11	2.99	3.80
Ramphastidae	*Selenidera maculirostris*	5	169.0	4.57	2.24	2.14
Cotingidae	*Carpornis cucullatus*	19	71.5	1.44	1.14	0.73
Cotingidae	*Lipaugus lanioides*	7	96.0	1.96	1.29	0.89
Cotingidae	*Tityra cayana*	6	71.0	2.15	1.36	1.19
Pipridae	*Chiroxiphia caudata*	40	25.0	0.88	0.80	0.54
Pipridae	*Ilicura militaris*	10	12.0	0.63	0.47	0.32
Pipridae	*Schiffornis virescens*	32	25.0	1.03	0.60	0.50
Tyrannidae	*Mionectes rufiventris*	71	14.0	1.07	0.59	0.40
Tyrannidae	*Myiodynastes maculatus*	1	45.0	2.08	1.25	0.84
Muscicapidae	*Platycichla flavipes*	20	59.0	1.78	1.00	0.75
Muscicapidae	*Turdus albicollis*	48	56.0	1.35	0.80	0.65
Muscicapidae	*Turdus rufiventris*	3	73.0	1.92	0.76	0.78
Emberizidae	*Cacicus haemorrhous*	1	33.0	1.90	0.60	0.90
Emberizidae	*Cissopis leveriana*	0	-	-	-	-
Emberizidae	*Euphonia pectoralis*	5	14.5	0.88	0.78	0.55
Emberizidae	*Habia rubica*	46	35.0	1.54	1.02	0.95
Emberizidae	*Orchesticus abeillei*	1	31.5	-	-	-
Emberizidae	*Orthogonys chloricterus*	2	38.0	1.75	0.90	0.82
Emberizidae	*Stephanophorus diadematus*	3	32.8	0.99	0.88	0.79
Emberizidae	*Tachyphonus coronatus*	8	27.0	1.50	0.85	0.80
Emberizidae	*Tangara cyanocephala*	1	14.0	0.91	0.63	0.51
Emberizidae	*Tangara desmaresti*	5	21.0	0.87	0.74	0.50
Emberizidae	*Tangara seledon*	1	18.0	0.96	0.73	0.59
Emberizidae	*Thraupis cyanoptera*	4	41.0	1.30	1.04	0.89
Emberizidae	*Thraupis ornata*	3	36.5	1.39	0.86	0.69
Emberizidae	*Trichothraupis melanops*	95	23.0	1.23	0.80	0.65

Appendix 2. 2.Tables of canonical correspondence analysis (CCA) of frugivores birds with fruit morphological variables in each plant family consumed.

```
AXIS SUMMARY STATISTICS
Number of canonical axes: 3
Total variance ("inertia") in the species data:   3.1474
----------------------------------------------------------
                                   Axis 1   Axis 2   Axis 3
----------------------------------------------------------
Eigenvalue                          0.303    0.271    0.150
Variance in species data
     % of variance explained          9.6      8.6      4.8
     Cumulative % explained           9.6     18.2     23.0
Pearson Correlation, Spp-Envt*      0.845    0.898    0.751
Kendall (Rank) Corr., Spp-Envt      0.524    0.363    0.276
----------------------------------------------------------
* Correlation between sample scores for an axis derived from the species
     data and the sample scores that are linear combinations of the
     environmental variables. Set to 0.000 if axis is not canonical.


            MONTE CARLO TEST RESULTS -- EIGENVALUES
-----------------------------------------------------------
                                 Randomized data
            Real data    Monte Carlo test,   99 runs
           ------------  --------------------------
  Axis      Eigenvalue   Mean    Minimum   Maximum       p
-----------------------------------------------------------
     1          0.303    0.239     0.125     0.365    0.1700
     2          0.271    0.153     0.077     0.281    0.0200
     3          0.150    0.102     0.052     0.196    0.0700
-----------------------------------------------------------
p = proportion of randomized runs with eigenvalue greater
    than or equal to the observed eigenvalue; i.e.,
p = (1 + no. permutations >= observed)/(1 + no. permutations)


CORRELATIONS AND BIPLOT SCORES for   6 morphology variables
------------------------------------------------------------------
                     Correlations*             Biplot Scores
    Variable      Axis 1  Axis 2  Axis 3    Axis 1  Axis 2  Axis 3
------------------------------------------------------------------
   1 frut mass     0.484   0.261   0.650     0.484   0.261   0.650
   2 seed mass     0.767   0.028  -0.113     0.767   0.028  -0.113
   3 pulp mass     0.370   0.287   0.753     0.370   0.287   0.753
   4 > fruit diam  0.737   0.078  -0.013     0.737   0.078  -0.013
   5 no. seed      0.142  -0.026  -0.338     0.142  -0.026  -0.338
   6 > seed diam   0.839   0.210   0.128     0.839   0.210   0.128
-----------------------------------------------------------------
* Correlations are "intraset correlations" of ter Braak (1986)
```

Appendix 2. 3. Tables of canonical correspondence analysis (CCA) of frugivores birds with fruit nutritional variables in each plant family consumed.

```
AXIS SUMMARY STATISTICS
Number of canonical axes: 3
Total variance ("inertia") in the species data:   2.7404
---------------------------------------------------------
                                  Axis 1   Axis 2   Axis 3
---------------------------------------------------------
Eigenvalue                         0.303    0.160    0.099
Variance in species data
     % of variance explained        11.1      5.8      3.6
     Cumulative % explained         11.1     16.9     20.5
Pearson Correlation, Spp-Envt*     0.860    0.815    0.678
Kendall (Rank) Corr., Spp-Envt     0.414    0.478    0.409
---------------------------------------------------------
* Correlation between sample scores for an axis derived from the species
     data and the sample scores that are linear combinations of the
     environmental variables. Set to 0.000 if axis is not canonical.
```

```
MONTE CARLO TEST RESULTS -- EIGENVALUES
----------------------------------------------------------
                            Randomized data
           Real data    Monte Carlo test,   99 runs
          ------------  --------------------------
  Axis     Eigenvalue    Mean    Minimum   Maximum       p
----------------------------------------------------------
     1         0.303    0.244     0.148     0.328   0.0800
     2         0.160    0.154     0.087     0.218   0.4200
     3         0.099    0.096     0.048     0.135   0.4200
----------------------------------------------------------
p = proportion of randomized runs with eigenvalue greater
    than or equal to the observed eigenvalue; i.e.,
p = (1 + no. permutations >= observed)/(1 + no. permutations)
```

```
CORRELATIONS AND BIPLOT SCORES for   4 nutritional variables
-----------------------------------------------------------------
                       Correlations*              Biplot Scores
    Variable       Axis 1  Axis 2  Axis 3     Axis 1  Axis 2  Axis 3
-----------------------------------------------------------------
   1 %protein      -0.622  -0.537   0.467     -0.622  -0.537   0.467
   2 %lipid        -0.738   0.581   0.080     -0.738   0.581   0.080
   3 %soluble sugar0.725  -0.214   0.478      0.725  -0.214   0.478
   4 %insol. sugar 0.235  -0.734  -0.233      0.235  -0.734  -0.233
---------------------------------------------------------------
* Correlations are "intraset correlations" of ter Braak (1986)
```

Appendix 4. Growth form, colour, and mean morphological and nutritional composition measures of fruits collected in Parque Estadual Intervales in southern São Paulo.

Family	Specie	Growth form	Fruit Colour*	No. seeds/ fruit	Seed width (mm)	Seed length (mm)	Fruit width (mm)	Fruit length (mm)	Fruit mass (g)	Total seeds mass (g)	One seed mass (g)	Pulp mass (g)	% Protein	% Lipid	% Soluble sugar	% Insoluble sugar
Acanthaceae	*Nendonea puberula*		black	1.0	8.54	14.05	11.42	14.69	1.200	0.198	0.198	1.002		9.25	12.47	10.79
Anacardiaceae	*Schinus terebinthifolius*	tree	pink	1.0	3.38	3.93	4.20	4.53	0.022	0.012	0.012	0.010				
Anacardiaceae	*Tapirira guianensis*	tree	black	1.0	11.14	17.55	13.47	19.75	1.228	0.220	0.220	1.008	6.39	6.05	1.09	11.04
Annonaceae	*Guatteria dusennii*	tree	black	1.0	4.79	8.83	6.86	10.82	0.364	0.098	0.098	0.266	13.25	9.24	12.44	10.81
Annonaceae	*Guatteria nigrescens*	tree	black	1.0	10.35	13.37	12.32	14.77	1.212	0.427	0.427	0.785	18.92	1.52	11.13	36.35
Annonaceae	*Rolinia* sp.	tree	gray	44.0			4.20	4.90	66.290	13.778	0.341	52.512				
Annonaceae	*Rollinia emarginata*	tree	gray		9.78	13.70				0.314	0.309					
Annonaceae	*Xylopia brasiliensis*	tree	white/ (a)	1.0	4.51	7.17	4.46	7.34	0.088	0.060	0.028	0.028				
Aquifoliaceae	*Ilex brevicuspis*	tree	red	4.1	1.88	3.23	3.49	3.92	0.049	0.020	0.008	0.029				
Aquifoliaceae	*Ilex microdonta*	tree		3.0	1.67	2.33	3.12	4.00	0.032	0.009	0.004	0.023				
Araceae	*Anthurium crassipes*	hemiepiphyt	yellow	1.8	1.44	2.18			0.010	0.004	0.002	0.006	7.97	7.45	17.91	31.62
Araceae	*Anthurium scandens*	hemiepiphyt	white	3.7	1.07	2.29	3.52	4.61	0.021	0.006	0.002	0.015				
Araceae	*Heteropsis cf. rigidifolia*	hemiepiphyt	white	2.3	1.11	2.24			0.075	0.002	0.012	0.073				
Araceae	*Heteropsis* sp.1	hemiepiphyt	orange	2.5	4.96	9.36	11.94	13.58	1.442	0.197	0.089	1.245	6.58	3.41	15.40	23.48
Araceae	*Heteropsis* sp.2	hemiepiphyt	orange		7.24	12.88					0.429					
Araceae	*Philodendron appendiculatum*	hemiepiphyt	pale green		0.46	0.98							5.26	17.19	13.32	21.19
Araliaceae	*Didymopanax angustissimum*	tree	brown	1.6	3.46	5.81	7.61	8.29	0.155	0.016	0.010	0.140	7.89			
Araliaceae	*Oreopanax* sp.	tree	purple	4.9	3.01	5.18	7.60	9.11	0.409	0.078	0.019	0.331				
Arecaceae	*Astrocaryum aculeatissimum*	tree	brown	1.0	12.08	15.93	18.73	20.29	4.648	1.254	1.254	3.394		9.80	15.60	22.80
Arecaceae	*Euterpe edulis*	tree	black	1.0	10.38	11.19	12.23	12.89	1.316	0.830	0.830	0.486		8.60	0.70	18.20
Arecaceae	*Geonoma gamiova*	scrub	black	1.0	7.88	9.09	10.96	11.79	0.881	0.309	0.309	0.572	12.45	1.90	0.80	28.10
Arecaceae	*Geonoma* sp.	scrub	black	1.0	6.12	6.28	8.11	8.56	0.442	0.164	0.164	0.278	12.69	6.20	1.30	13.20
Bignoniaceae	*Adenocalymma* sp.	liana	orange	1.0	9.35	17.45	21.20	22.50	9.173	0.961	0.961	8.213	8.19	3.30	1.60	6.50
Boraginaceae	*Cordia corymbosa*	tree	red	1.0	2.88	3.84	3.37	4.01	0.083	0.020	0.020	0.064				
Boraginaceae	*Tournefortia cf. paniculata*	liana	red	3.7	2.20	3.57	4.54	5.18	0.145	0.017	0.005	0.128	4.45	2.51	18.06	15.80
Bromeliaceae	*Bromeliaceae 1*	epiphyt		97.6	0.37	1.06	4.47	10.87	0.178	0.030	<0.001	0.148				
Bromeliaceae	*Bromeliaceae 2*	epiphyt	yellow	32.7	1.40	2.64	6.63	16.65	0.311	0.060	0.002	0.251				
Burseraceae	*Protium heptaphyllum*	tree	red	1.0	9.25	17.48	11.14	18.65	1.490	0.195	0.194	1.295	6.64			
Cactacea	*Rhipsalis eliptica*	epiphyt	pink	14.3	0.69	1.22	5.69	8.86	0.229	0.004	<0.001	0.225	2.71	6.07	5.41	9.55
Cactaceae	*Rhipsalis campos portuana*	epiphyt	pink	27.5	0.61	1.49	5.34	7.66	0.182	0.007	<0.001	0.175	5.52	6.50	0.60	26.80
Cactaceae	*Rhipsalis puniceo-descus*	epiphyt	yellow	1.0	4.65	5.30	5.78	8.10	0.302	0.032	0.042	0.270				
Cactaceae	*Rhipsalis* sp.	epiphyt	pink	15.7	0.63	1.50	7.78	9.53	0.425	0.014	<0.001	0.411				
Cecropiaceae	*Cecropia glaziovi*	tree	orange	2964.0	1.37	2.40	11.20	147.60	14.870	5.133	0.001	9.737	12.09	3.71	0.76	7.68
Cecropiaceae	*Coussapoa microcarpa*	tree	yellow	37.3	1.54	2.57	5.14	8.34	0.259	0.060	0.002	0.199	12.40	2.27	0.54	6.91

Family	Specie	Growth form	Fruit Colour*	No. seeds/ fruit	Seed width (mm)	Seed length (mm)	Fruit width (mm)	Fruit length (mm)	Fruit mass (g)	Total seeds mass (g)	One seed mass (g)	Pulp mass (g)	% Protein	% Lipid	% Soluble sugar	% Insoluble sugar
Celastraceae	*Maytenus robusta*	tree	white/yellow (a/c)	1.1	6.32	10.86	7.84	12.01	0.299	0.071	0.120	0.228				
Chrysobalanaceae	*Licania kuntiana*	tree	gray	1.0	11.94	19.63	15.67	21.63	2.833	0.843	0.843	1.990				
Clethraceae	*Clethra scabra*	tree		1.1	4.63	5.38	11.83	12.53	0.984	0.048	0.044	0.936	5.30	6.42	7.91	5.96
Clusiaceae	*Clusia criuva*	scrub	orange (a)	9.2	1.52	3.85	4.43	8.47	0.092	0.048	0.005	0.044	4.69	65.82	1.79	3.07
Commelinaceae	*Dichorisandra thyrsiflora*	herb	White/ red (a/c)	1.0	8.71	9.78	10.31	10.93	0.591	0.419	0.419	0.173		5.20	7.40	13.10
Commelinaceae	*Tradescandia* sp.	herb	Orange (a)	5.3	3.20	3.76	6.27	11.61	0.303	0.106	0.025	0.197		8.30	14.00	11.60
Cucurbitaceae	*Wilbrandia hibiscoides*		Red	11.1	7.85	13.95	24.94	32.25	10.491	1.608	0.159	8.883				
Elaeocarpaceae	*Sloanea monosperma*	tree	Orange	1.0	9.23	13.87	10.03	14.73	1.230	0.482	0.482	0.747				
Erythroxylaceae	*Erythroxylum ambiguum*	tree	Red	1.0	3.11	6.27	5.49	7.51	0.168	0.033	0.051	0.136				
Euphorbiaceae	*Alchornea triplinervia*	tree	Red	2.0	4.56	4.95	5.00	5.83			0.039		8.00	65.75	1.49	6.52
Euphorbiaceae	*Croton floribundus*	tree		3.0	1.30	2.80										
Euphorbiaceae	*Hyeronima alchorneoides*	tree	Black	1.0	2.74	3.67	3.17	4.27	0.042	0.019	0.019	0.024				
Euphorbiaceae	*Sapium glandulatum*	tree	Red	1.0	5.80	6.07	5.74	6.03	0.090	0.069	0.069	0.021				
Euphorbiaceae	*Tetrorchidium rubrivenium*	tree	Red	1.0	4.58	5.84	4.62	6.20	0.518	0.312	0.312	0.206	7.49	59.55	3.14	5.52
Flaucourtiaceae	*Casearia decandra*	tree	Yellow	4.6	4.75	6.31	11.57	12.24	1.243	0.111	0.029	1.133	5.29	2.78	7.82	16.06
Flaucourtiaceae	*Casearia sylvestris*	tree	Orange	4.0	1.37	1.99	6.00	4.00			0.003					
Flaucourtiaceae	*Prockia crucis*	tree		8.0	0.87	1.30	5.67	5.93	0.130	0.018	0.002	0.111				
Gesneriaceae	*Codonantha cordifolia*	epiphyt	Orange	95.6	0.30	0.80	8.53	10.11	0.328	0.014	<0.001	0.315				
Heliconiaceae	*Heliconia velloziana*	hemiepiphyt	blue/red (f/b)	1.4	5.64	10.59	8.74	14.09	0.745	0.208	0.144	0.537	8.28	24.36	2.93	13.25
Hippocrateaceae	*Cheiloclinum cognatum*	liana	Yellow	3.3	13.72	21.62	32.97	35.02	18.060	3.307	0.928	14.752	6.23	2.98	1.11	10.80
Hippocrateaceae	*Peritassa hatschbachii*	liana	Gray	1.0	13.25	20.83	19.10	23.80	4.316	1.281	1.281	3.035				
Humiriaceae	*Vantanea af. Compacta*	tree	Orange	1.0	11.39	19.79	14.66	22.48	3.224	1.317	1.370	1.907	4.49	20.67	0.71	4.75
Icacimaceae	*Citronella af. Megaphylla*	tree	Black	1.0	12.52	18.87	14.55	20.20	2.965	1.022	1.022	1.943	11.16	26.28	1.96	9.20
Lauraceae	*Cryptocarya moschata*	tree	Yellow	1.0	15.07	17.22	19.09	20.39	4.954	1.617	1.617	3.336	10.73	30.83	24.17	13.37
Lauraceae	*Lauraceae* sp.1	tree		1.0									17.00	20.48	1.20	5.94
Lauraceae	*Lauraceae* sp.2	tree	Brown	1.0	11.42	11.52	14.34	15.94	2.487	0.865	0.865	1.623				
Lauraceae	*Nectandra grandiflora*	tree	Black	1.0	10.00	16.25	12.50	22.50								
Lauraceae	*Nectandra membranacea var. cuspidata*	tree	Green	1.0	8.55	9.45	8.48	10.85	0.741	0.333	0.333	0.409				
Lauraceae	*Ocotea aeciphila*	tree	Brown	1.0	8.33	8.53	10.73	11.07	0.786	0.243	0.243	0.543	9.53	21.60	0.70	6.20
Lauraceae	*Ocotea catharinensis*	tree	Black	1.0	8.10	15.00	18.80	30.00	4.285	0.272	0.272	4.013				
Lauraceae	*Ocotea cf. bicolor*	tree	Black	1.0	9.69	10.16	12.21	12.56	1.239	0.420	0.420	0.819				
Lauraceae	*Ocotea odorifera*	tree	Black	1.0	8.06	17.38	10.92	19.16	1.491	0.361	0.361	1.130				
Lauraceae	*Ocotea pulchella*	tree	Black	1.0	5.40	8.50	6.75	9.40	0.239	0.121	0.121	0.119				
Lauraceae	*Ocotea* sp.	tree		1.0	9.40	15.30	12.00	18.50	1.894	0.468	0.468	1.426	14.03	29.50	1.58	9.10

Family	Specie	Growth form	Fruit Colour*	No. seeds/ fruit	Seed width (mm)	Seed length (mm)	Fruit width (mm)	Fruit length (mm)	Fruit mass (g)	Total seeds mass (g)	One seed mass (g)	Pulp mass (g)	% Protein	% Lipid	% Soluble sugar	% Insoluble sugar
Lauraceae	*Ocotea teleiandra*	tree	Black	1.0	12.48	23.26	14.28	25.84	3.672	1.614	1.614	2.058	21.68	20.20	0.60	8.60
Lauraceae	*Persea pyrifolia*	tree	Black	1.0	12.60	13.75	15.61	18.03	3.424	1.438	1.438	1.985	7.59	53.20	2.20	6.30
Leg. Papilionoideae	*Andira pisonis*	tree	Green	1.0	22.17	26.15	25.11	28.50	11.792	6.901	6.903	4.891				
Leg. Papilionoideae	*Dalbergia sp.*	tree			3.04	5.17					0.015					
Leg. Papilionoideae	*Ormosia arborea*	tree	Red	1.0	15.66	18.09					2.049					
Liliaceae	*Smilax elastica*	liana	Purple	1.9	5.87	6.49	10.50	12.59	1.007	0.307	0.126	142.857	8.73	2.24	0.42	11.60
Liliaceae	*Smilax* sp.	liana	Red	1.6	5.64	6.04				0.118	0.077					
Loranthaceae	*Psittacanthus* sp.	hemiparasite	Red	1.0	6.10	8.78	9.33	13.72	0.736	0.068	0.145	0.668	7.80	14.66	0.72	11.56
Loranthaceae	*Struthanthus concinus*	hemiparasite	Gray	1.0	2.52	3.82	3.81	4.49	0.043	0.014	0.012	0.029				
Loranthaceae	*Struthanthus vulgaris*	hemiparasite	Black	1.0	2.50	4.83	4.35	6.73	0.114	0.022	0.022	0.092				
Magnoliaceae	*Talauma ovata*	tree	Red	1.0	10.13	11.69	10.17	12.21	0.544	0.279	0.279	0.265	7.32	52.59	0.42	6.99
Malpighiaceae	*Bunchosia ghuminensis*			1.0	8.30	10.75	18.45	20.80	3.957	0.604	0.604	3.353				
Malpighiaceae	*Byrsonima* sp.	tree	Red	1.0	7.71	10.84	11.00	13.82	1.567	0.246	0.246	1.320		1.06	0.34	11.67
Marcgraviaceae	*Marcgravia polyantha*	liana	Red	3057.4	0.40	1.04	8.45	9.82	0.467	0.163	0.027	0.304	8.11	2.00	0.50	3.90
Marcgraviaceae	*Noranthea brasiliensis*	epiphyt	Purple	64.0	1.30	4.66	11.20	14.00	1.392	0.196	0.004	1.196				
Melastomataceae	*Leandra australis*	scrub	Purple	56.1	0.97	0.91	7.66	8.49	0.307	0.006	<0.001	0.301				
Melastomataceae	*Leandra barbinervis*	tree	Black	477.5	0.40	0.93	7.12	7.50	0.199	0.025	<0.001	0.174	12.12			
Melastomataceae	*Leandra cf laevigata*	scrub	Black	1225.4	0.30	0.52	7.01	6.85	0.239	0.014	<0.001	0.225	13.28			
Melastomataceae	*Leandra cf sabiaensis*	scrub	Lilic	261.8	0.26	0.58	6.65	7.56	0.135	0.005	<0.001	0.130	8.46			
Melastomataceae	*Leandra cf. pilonensis*	tree		27.0	0.51	0.92	5.70	6.30	0.078	0.002	<0.001	0.077				
Melastomataceae	*Leandra cf. refracta*		Black	826.2	0.30	0.50	7.98	8.42	0.327	0.011	<0.001	0.316				
Melastomataceae	*Leandra cordifolia*	scrub	Black	389.0	0.43	0.78	4.70	7.47	0.154	0.019	<0.001	0.134				
Melastomataceae	*Leandra dasytricha*	scrub	Black	518.4	0.21	0.33	5.12	6.08	0.090	0.008	<0.001	0.081	6.52	4.56	13.32	25.38
Melastomataceae	*Leandra echinata*		Purple	1016.4	0.43	0.71	10.15	11.96	0.961	0.040	<0.001	0.922	3.05			
Melastomataceae	*Leandra fragilis*	scrub	Purple	95.3	0.37	0.62	3.96	6.46	0.038	0.007	<0.001	0.031	7.21	2.04	1.27	10.99
Melastomataceae	*Leandra melastomatoides*	scrub	Purple	241.4	0.35	0.97	9.44	13.33	0.698	0.029	<0.001	0.669	5.24	1.97	32.65	21.46
Melastomataceae	*Leandra pilonensis*	tree	Purple	127.8	0.48	1.14	6.99	9.45	0.233	0.013	<0.001	0.219				
Melastomataceae	*Leandra regnellii*	scrub	Black	623.9	0.21	0.31	7.22	8.72	0.288	0.008	<0.001	0.280	7.01	2.39	25.19	34.75
Melastomataceae	*Leandra* sp.1			86.0	0.48	0.91	9.68	10.79	0.535	0.011	<0.001	0.524				
Melastomataceae	*Leandra* sp.2	scrub	Purple	39.2	0.50	1.16	6.78	7.18	0.199	0.007	<0.001	0.191	8.42	2.27	19.88	12.75
Melastomataceae	*Leandra xanthocona*	scrub	Purple	256.8	0.57	0.88	10.79	11.54	0.928	0.017	<0.001	0.924	5.71	3.46	32.99	34.79
Melastomataceae	*Miconia budlejoides*	tree	Black	16.6	1.01	1.27	4.37	5.62	0.088	0.021	0.004	0.067	8.74	1.81	1.27	5.11
Melastomataceae	*Miconia cabucu*			6.5	1.65	2.68	3.95	5.23	0.103	0.027	0.012	0.076				
Melastomataceae	*Miconia cf. doriana*	scrub	Black	3.0	1.77	2.24	4.29	5.63	0.106	0.027	0.008	0.079				
Melastomataceae	*Miconia cinnamomifolia*	tree	Purple		0.80	1.20	3.30	4.00								
Melastomataceae	*Miconia cubatanensis*	tree	Black	1.0	2.25	2.35	4.65	5.20	0.058	0.002	0.002	0.056				
Melastomataceae	*Miconia descolor*	tree	Blue	9.2	0.92	1.28	3.60	4.20	0.067	0.013	0.003	0.053				
Melastomataceae	*Miconia inconspicua*	tree	Blue	13.8	0.86	1.13	3.04	3.62	0.042	0.002	<0.001	0.040				

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Melastomataceae	*Miconia latecrenata*	scrub		17.0	0.40	0.62	2.50	2.70	0.009	0.001	<0.001	0.001				
Melastomataceae	*Miconia pusilliflora*	tree	Black	2.6	2.08	3.01	4.73	5.27	0.063	0.007	0.007	0.057	14.12	11.10	8.90	7.00
Melastomataceae	*Miconia racemifera*	tree	Purple	20.8	1.21	1.64	3.93	4.60	0.048	0.016	0.003	0.033				
Melastomataceae	*Miconia sellowiana*	tree	Purple	12.6	0.61	1.15	4.00	4.41	0.055	0.006	0.001	0.053				
Melastomataceae	*Miconia* sp.	scrub	Black	14.2	1.01	1.40	4.36	4.90	0.094	0.020	0.003	0.074				
Melastomataceae	*Miconia theaezans*	scrub	Purple	24.4	0.45	0.63	2.96	3.35	0.018	0.002	0.155	0.017	12.85	9.20	4.70	4.10
Melastomataceae	*Miconia tristis*	tree	Blue	6.5	1.28	2.11	3.55	4.00	0.114	0.007	0.002	0.107				
Melastomataceae	*Miconia valtherii*	tree	Purple	38.9	0.51	0.75	3.93	4.41	0.063	0.007	<0.001	0.056	7.04	4.34	10.07	13.13
Melastomataceae	*Ossaea amygdaloides*	scrub	Purple	85.7	0.56	1.05	6.55	7.43	0.182	0.008	<0.001	0.173				
Meliaceae	*Cabralea canjerana*	tree	Orange (a)	1.8	6.00	8.08	9.73	17.38	0.920	0.237	0.139	0.682			2.30	
Meliaceae	*Guarea macrophylla*	tree	Red	1.0	8.15	9.55	7.83	10.43	0.463	0.286	0.286	0.177				
Menispermaceae	*Abuta sellowiana*	liana	Yellow	1.0	12.23	24.99	16.24	28.89	4.333	1.244	1.251	3.089				
Menispermaceae	*Cissampelos andromorpha*		Red	1.0	5.27	6.28	7.78	8.18	0.211	0.028	0.028	0.183				
Mimosaceae	*Inga marginata*	tree	Green	1.0	6.46	10.10	7.60	11.87	0.641	0.205	0.205	0.436	9.49	1.54	12.16	36.36
Mimosaceae	*Inga sessilis*	tree	White	1.0	8.57	15.71	14.28	20.00					13.62	0.82	4.19	12.25
Mimosaceae	*Inga striata*	tree	White	1.0	8.89	12.74	11.33	15.58	0.850	0.433	0.423	0.416				
Mimosaceae	*Inga vulpina*	tree	Yellow	1.0	11.31	16.73	12.07	16.29	1.843	0.560	0.560	1.283	4.03	2.76	20.21	53.31
Monimiaceae	*Hennecartia cf. omphalandra*		Black	1.0	1.65	11.86	12.86	14.24	1.346	0.911	13.800	0.435	9.18	19.65	13.39	30.35
Monimiaceae	*Mollinedia af. uleana*	tree	Green	1.0	8.60	15.60	10.50	19.22	1.340	0.184	0.184	1.156	19.75	12.12	1.27	4.56
Monimiaceae	*Mollinedia boracensis*	tree	Green	1.0	10.17	16.59	13.12	19.75	2.155	0.850	0.850	1.305	7.78	4.06	0.12	6.47
Monimiaceae	*Mollinedia floribunda*	tree	Black	1.0	5.38	6.50	7.02	7.50	0.253	0.104	0.104	0.149	13.58			
Moraceae	*Ficus insipida*	tree	Green	107.5	1.50	2.45	20.45	24.20	5.584	0.194	0.003	5.391	5.13	5.98	0.42	9.17
Moraceae	*Ficus luschnatiana*	tree	Green/ Red	49.9	0.92	1.11	12.33	14.54	1.804	0.020	0.047	1.784	8.62	4.28	4.60	10.27
Moraceae	*Ficus* sp 2	tree	Green	157.1	0.96	1.27	15.55	16.65	2.474	0.105	0.002	2.369	3.50	5.78	6.59	13.61
Moraceae	*Sorocea bonplandii*	tree	Red	1.0	5.14	6.10	8.42	9.84	0.431	0.096	0.096	0.335				
Myristicaceae	*Virola bicuhyba*	tree	Red	1.0	13.40	23.40	21.00	36.80	7.993	1.557	1.557	6.436	6.67			
Myrsinaceae	*Ardisia guyanensis*	scrub	Red	1.0	6.11	6.34	7.17	7.72	0.348	0.081	0.081	0.268				
Myrsinaceae	*Cybianthus peruvianus*	tree	Red	1.0	3.27	3.46	5.29	5.97	0.129	0.026	0.026	0.103	7.49	0.85	0.93	15.43
Myrsinaceae	*Myrsine coriacea*	tree	Black	1.0	2.96	2.99	3.27	3.42	0.025	0.012	0.013	0.013		50.80	1.20	4.20
Myrsinaceae	*Myrsine gardneriana*	scrub		1.0	4.47	4.60	4.81	4.96	0.065	0.043	0.043	0.022	8.98	11.88	3.15	11.77
Myrsinaceae	*Myrsine lancifolia*	tree	Purple	1.0	3.88	4.02	4.07	4.11	0.047	0.019	0.019	0.028				
Myrsinaceae	*Myrsine umbellata*	tree	Black	1.0	2.95	3.10	3.16	3.36	0.022	0.016	0.016	0.006				
Myrsinaceae	*Myrsine venesa*	scrub	Black	1.0	4.10	4.18	4.31	4.44	0.046	0.034	0.034	0.013		5.51	2.05	10.97
Myrtaceae	*Calycorectes australis*	tree	Red	1.0	8.30	10.80	13.60	13.90	1.494	0.315	0.315	1.179				
Myrtaceae	*Calyptranthes* sp.	tree	Red	1.0	5.55	6.08	5.67	6.24	0.127	0.104	0.104	0.023				

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Myrtaceae	*Campomanesia guaviroba*	tree	Yellow	7.3	4.84	5.41	19.86	21.41	5.212	0.098	0.025	5.114	4.33	4.40	17.71	27.11
Myrtaceae	*Campomanesia neriflora*	tree	Green	12.2	5.10	6.95	19.35	22.76	6.281	0.423	0.032	5.858	5.42	8.73	12.60	15.69
Myrtaceae	*Campomanesia xanthocarpa*	tree	Yellow	6.4	3.98	4.80	14.09	15.91	2.300	0.069	0.022	2.231	7.65	4.13	13.14	13.89
Myrtaceae	*Eugenia cuprea*	tree	Red	1.0	9.05	11.50				0.521	0.521					
Myrtaceae	*Eugenia melanogyna*	tree	Red	1.0	17.94	24.72	24.74	37.66	15.849	2.902	2.902	12.946	3.79	3.48	11.19	8.61
Myrtaceae	*Eugenia mosenii*	tree	Gray	1.0	10.73	12.31	12.99	19.02	2.842	0.668	0.639	2.174	11.35	20.50	6.50	8.00
Myrtaceae	*Eugenia* sp.1	tree	Green	1.0	17.22	17.38				1.712	1.712					
Myrtaceae	*Eugenia* sp.2	tree	Orange	1.0	12.19	15.42				1.158	1.158					
Myrtaceae	*Eugenia stictosepala*	tree	Orange	1.3	12.10	16.47	15.24	21.11	3.567	1.282	1.282	2.286		11.70	6.10	11.10
Myrtaceae	*Gomidesia affins*	tree	Red	1.0	6.44	7.13	15.00	16.29	2.385	0.050	0.049	2.336	4.72	4.52	9.05	10.29
Myrtaceae	*Gomidesia cf. schaueriana*	tree	Red	1.8	5.05	5.96	10.93	14.01	1.495	0.085	0.058	1.410	3.72	2.82	1.17	5.96
Myrtaceae	*Gomidesia fenzliana*	tree		3.6	3.75	5.07	10.00	12.20	0.991	0.090	0.024	0.902	14.83	13.09	4.88	15.76
Myrtaceae	*Marlierea reitzii*	tree	Purple	1.0	8.90	10.14	14.76	17.97	1.931	0.274	0.274	1.656	6.44	11.57	0.99	7.07
Myrtaceae	*Marlieria eugeniopsoides*	tree		1.8	11.66	22.30	21.85	34.34	7.783	1.871	0.977	5.912	5.00	6.64	19.40	13.32
Myrtaceae	*Myrcia fallax*	tree	Black	1.5	4.24	5.13	6.61	7.61	0.211	0.049	0.039	0.161	11.43	14.46	7.55	19.89
Myrtaceae	*Myrcia grandiflora*	tree	Yellow	2.6	8.00	9.17	15.86	18.93	3.085	0.438	0.188	2.647	6.08	8.40	22.80	6.70
Myrtaceae	*Myrcia rufula*	tree	Yellow	1.8	5.20	9.21	10.38	14.66	0.971	0.187	0.102	0.784	8.67	16.50	30.60	5.00
Myrtaceae	*Myrcia* sp.1	tree		3.5	5.07	7.21	12.90	15.59	1.986	0.291	0.089	1.695	6.91	4.80	3.65	21.86
Myrtaceae	*Myrcia* sp.2	tree		1.0	13.77	15.23	20.76	22.30	5.350	0.679	0.679	4.671	7.94	1.51	1.84	8.49
Myrtaceae	*Neomitrantes glomerata*	tree	Black	1.0	3.80	4.58	5.70	7.02	0.136	0.047	0.047	0.090				
Myrtaceae	*Plinia plicato-costata*	tree	Black	1.0	6.20	10.20	12.20	13.25	1.409	0.270	0.270	1.140				
Myrtaceae	*Psidium cattleianum*	tree	Yellow	58.9	4.12	6.12	26.72	29.02	13.023	0.491	0.009	12.533	3.21	5.12	17.44	15.57
Myrtaceae	*Psidium guajava*	tree	Yellow	170.2	3.15	3.77	57.02	59.38	97.197	2.312	0.017	94.885	4.79	2.03	18.22	20.87
Myrtaceae	*Psidium* sp.	tree	Red	1.3	6.90	10.07	13.90	16.00	2.166	0.273	0.215	1.893	4.64	3.60	13.90	11.70
Myrtaceae	*Siphoneugena densiflora*	tree	Purple	3.2	7.36	9.49	12.98	15.90	1.720	0.234	0.154	1.487	8.70	5.20	27.00	6.50
Nyctaginaceae	*Guapira opposita*	tree	Black/red (f/p)	1.0	3.60	6.70	5.30	8.75	0.124	0.032	0.032	0.092	19.10	4.08	5.94	9.27
Ochnaceae	*Ouratea vaccinioides*	tree	Black	1.4	4.34	6.55	5.13	7.73	0.139	0.052	0.042	0.087	9.79	8.82	2.13	10.22
Olacaceae	*Heisteria silvianii*	tree	White/red (f/b)	1.0	9.30	14.55	10.15	15.30	1.834	0.501	0.501	1.333				
Olacaceae	*Scoepfia brasiliensis*	tree	Black				11.23	14.12	1.017					3.99	0.35	28.13
Olacaceae	*Tetrastylidium grandiflorum*	tree	Yellow	1.0	18.22	23.63	23.31	26.27	9.750	3.073	3.073	6.677	11.17	5.33	5.06	4.38
Onagraceae	*Fuchsia regia*	liana	Purple	11.6	1.20	2.59	4.69	16.30	0.331	0.027	0.003	0.304				
Onagraceae	*Fuchsia* sp.	liana	Purple	22.0	1.20	2.40				0.013	0.005					
Opiliaceae	*Agonandra* sp.	tree	Yellow	1.0	15.80	20.06	27.58	31.60	13.317	1.661	1.661	11.656				
Passifloraceae	*Passiflora amenthstina*	liana	Purple	92.9	3.64	5.99	35.86	37.82	22.747	1.751	0.020	21.104	6.11	0.69	0.11	9.92
Passifloraceae	*Passiflora capsularis*	liana	Pink	128.0	2.01	3.45	18.30	51.60	7.241	0.418	0.005	6.823				

Family	Specie	Growth form	Fruit Colour*	No. seeds/ fruit	Seed width (mm)	Seed length (mm)	Fruit width (mm)	Fruit length (mm)	Fruit mass (g)	Total seeds mass (g)	One seed mass (g)	Pulp mass (g)	% Protein	% Lipid	% Soluble sugar	% Insoluble sugar
Phytolaccaceae	*Phytolacca dioica*	tree	Yellow	8.7	1.78	2.09	4.58	8.85	0.225	0.031	0.006	0.194	8.20	3.89	9.04	39.03
Piperaceae	*Piper aduncum*	scrub	Green	475.5	0.55	0.80				0.043	0.001					
Piperaceae	*Piper corintoanum*	scrub	Green	588.0	1.07	1.33				0.334	0.001					
Piperaceae	*Piper dilatum*	scrub	Green	296.0	0.80	0.90				0.024	<0.001					
Piperaceae	*Piperaceae*	scrub	Green										5.47	21.44	1.31	12.52
Poaceae	*Poaceae*	herb		1.0	1.95	3.46	2.27	3.59	0.004	0.003	0.003	0.001				
Rhamnaceae	*Colubrina glandulosa*		Black	1.0	9.10	13.41	14.73	16.90	2.415	0.358	0.344	2.058	4.56	1.28	5.00	35.44
Rhamnaceae	*Rhamnus sphaerosperma*	tree	Black	1.0	3.11	6.27	5.49	7.51	0.168	0.033	0.051	0.136				
Rosaceae	*Prunus myrtifolia Koehne*	tree	Black	1.0	8.71	9.76	10.31	10.93	0.591	0.419	0.419	0.173				
Rosaceae	*Pyracanthea*	scrub	Red	5.0	0.98	1.59	5.03	8.88	0.324	0.020	0.003	0.304				
Rosaceae	*Rosaceae*			4.8	1.62	2.44	8.04	8.38	0.188	0.012	0.006	0.176				
Rosaceae	*Rubus brasiliensis*	scrub	Green	37.9	2.18	3.69	11.80	13.12	1.279	0.170	0.008	1.109				
Rosaceae	*Rubus rosaefolius*	herb	Red	283.3	0.89	1.55	10.78	13.31	0.991	0.108	<0.001	0.882	11.40	2.90	4.10	15.80
Rosaceae	*Rubus* sp.	herb		34.2	1.19	2.04	7.17	9.13	0.401	0.025	0.002	0.376				
Rosaceae	*Rubus urticaefolius*	scrub	Black	43.9	1.26	2.02	7.87	9.49	0.441	0.040	0.003	0.401				
Rubiaceae	*Alibertia mycifolia*	tree	Red	7.3	3.40	4.37	17.40	19.20	3.743	0.128	0.019	3.616	8.14			
Rubiaceae	*Amaioua intermedia*	tree	Black	10.4	3.45	4.40	9.01	14.51	0.656	0.130	0.013	0.527				
Rubiaceae	*Chamelia catharinae*	tree	Black	1.0	2.78	9.41	5.52	11.42	0.208	0.044	0.044	0.164	7.36	26.83	16.00	13.33
Rubiaceae	*Coccocypselum krauseanum*	herb	Blue	42.5	1.24	1.37	10.11	10.81	0.505	0.014	<0.001	0.491	5.79	2.38	0.81	2.90
rubiaceae	*Coccosypselum hasserianum*	herb	Blue	42.2	1.08	1.25	11.48	17.90	0.481	0.039	<0.001	0.443				
Rubiaceae	*Coussarea contracta*	tree	Red	1.0	10.65	12.83	16.08	17.43	2.385	0.413	0.413	1.973	8.55	2.32	10.62	12.25
Rubiaceae	*Galium hypocarpium*	herb	Orange	2.0	1.19	1.85	2.18	2.95	0.007	0.004	0.002	0.003	13.21	3.75	18.57	25.61
Rubiaceae	*Ixora heterodoxa*	tree	Black	1.4	2.19	3.22	8.47	16.16	0.835	0.060	0.054	0.775	10.12	5.50	9.80	6.00
Rubiaceae	*Posoqueria latifolia*	tree	Yellow	10.0	9.23	11.90	31.11	33.06	18.526	5.222	0.623	13.303	6.11	4.40	34.88	15.07
Rubiaceae	*Psychotria forsterosnoides*	scrub	Black	2.0	2.80	3.60	3.90	5.00	0.037	0.015	0.009	0.022				
Rubiaceae	*Psychotria longipes*	scrub	Black	2.0	2.90	4.38	5.30	5.30	0.105	0.020	0.010	0.085	11.29	2.51	8.44	30.92
Rubiaceae	*Psychotria* sp.1	scrub	Red	1.9	3.40	4.49	4.97	6.02	0.115	0.027	0.012	0.089	10.41	2.93	23.21	26.62
Rubiaceae	*Psychotria* sp.2		Green	1.0	2.75	3.77	2.89	3.69	0.017	0.009	0.009	0.008				
Rubiaceae	*Psychotria suterella*	tree	Blue	2.0	3.87	4.89	9.74	11.98	0.588	0.037	0.020	0.551	7.10	1.81	8.89	17.29
Rubiaceae	*Psychotria vellosiana*	scrub	Black	2.4	2.96	3.69	4.14	5.74	0.109	0.022	0.012	0.087		2.68	8.64	15.03
Rubiaceae	*Rudgea jasminoides*	tree	Red/ Yellow	2.0	4.35	6.25				0.034	0.017					
Rubiaceae	*Sabicea* sp.	herb	Blue	1.6	2.87	4.67	4.41	5.93	0.107	0.021	0.021	0.086		1.41	24.31	20.65
Rubiaceae	*Psychotria leiocarpa*	scrub	Black	2.0	2.34	2.57	2.58	4.24	0.026	0.009	0.005	0.017				
Sapindaceae	*Allophyllus edulis*	tree	Red	1.0	5.56	7.85	7.76	8.66	0.373	0.088	0.088	0.285	6.14	1.21	3.52	30.87
Sapindaceae	*Cupania vernalis*	tree	Yellow	1.0	7.56	11.73	8.36	14.66	0.694	0.294	0.294	0.400	14.54	55.60	1.50	8.90

Family	Specie	Growth form	Fruit Colour*	No. seeds/ fruit	Seed width (mm)	Seed length (mm)	Fruit width (mm)	Fruit length (mm)	Fruit mass (g)	Total seeds mass (g)	One seed mass (g)	Pulp mass (g)	% Protein	% Lipid	% Soluble sugar	% Insoluble sugar
Sapindaceae	*Matayba guianensis*	tree	White	1.0	5.26	8.04	5.76	8.96	0.234	0.094	0.103	0.140	8.78			
Sapotaceae	*Chrysophyllum dusenii*	tree	Purple	1.0	7.20	21.11	10.92	31.53	2.392	0.288	0.288	2.105	4.87	12.31	30.46	21.25
Sapotaceae	*Chrysophyllum sp.*	tree	Yellow	2.0	9.15	23.25	25.10	27.95	7.397	0.979	0.489	6.419	14.40	3.34	4.47	27.72
Simarubaceae	*Picramnia ramiflora*	scrub	Black	1.5	7.70	9.40				0.533	0.259					
Solanaceae	*Aureliana fasciculata*	tree		46.8	2.55	2.93	8.35	9.23	0.428	0.037	0.001	0.391				
Solanaceae	*Cestrum cf. laevigatum*		Black	4.8	3.36	7.00	9.34	17.80	0.818	0.091	0.022	0.727				
Solanaceae	*Solanaceae*	scrub	Orange	9.0	1.53	1.79				0.035	0.003					
Solanaceae	*Solanum americanum*	scrub	Yellow	7.9	1.82	2.32	3.49	4.48	0.089	0.017	0.005	0.072				
Solanaceae	*Solanum inodorum*	liana	Red	10.7	3.19	3.92	10.21	12.32	1.007	0.026	0.002	0.981	12.69	4.60	12.10	11.80
Solanaceae	*Solanum megalochiton*	tree	Purple	12.0	2.77	3.52	6.28	7.57	0.183	0.022	0.006	0.160	18.08	10.60	10.40	5.50
Solanaceae	*Solanum nigrum*	herb	Black	70.3	0.92	1.38	6.13	7.08	0.224	0.016	0.003	0.208				
Solanaceae	*Solanum phyllosepalum*		White/ Black	99.3	2.67	2.90	11.47	15.00	1.007	0.153	0.003	0.854				
Solanaceae	*Solanum pseudo-quina*	tree	Pale/ Green	64.0	2.60	3.15	14.23	14.60	2.017	0.095	0.005	1.922				
Solanaceae	*Solanum rufescens*	tree		34.1	3.02	3.56	11.28	12.05	1.087	0.081	0.006	1.006	17.62	13.60	9.10	5.80
Solanaceae	*Solanum sancta-catharinae*	tree	Black		2.43	3.18					0.001					
Solanaceae	*Solanum swartzianum*	tree	Yellow	14.0	2.76	3.96	10.66	11.83	0.886	0.097	0.002	0.789	18.16			
Solanaceae	*Solanum variabile*	scrub	Yellow	36.2	2.97	3.76	12.78	14.16	1.694	0.255	0.010	1.440				
Solanaceae	*Vassobia breviflora*		Orange	89.8	1.53	1.90	8.98	11.88	0.894	0.062	0.001	0.833				
Symplocaceae	*Symplocos glanduloso-marginata*	tree	Black	1.0	3.58	8.56	6.90	9.00	0.248	0.062	0.062	0.186	12.25	3.86	0.29	4.49
Symplocaceae	*Symplocos tetrandra*	tree	Black	1.0	4.53	13.28	7.91	15.63	0.649	0.147	0.147	0.502		3.20	4.50	7.50
Symplocaceae	*Symplocos variabilis*	tree	Green	1.0	6.45	16.85	8.25	17.95	0.868	0.223	0.223	0.645				
Ulmaceae	*Trema micrantha*	tree	Orange	1.0	1.83	2.08	2.20	2.53	0.010	0.004	0.004	0.006	10.74	48.76	0.13	2.10
Urticaceae	*Urera baccifera*	scrub	White/red (f/p)	1.3	1.97	3.00	1.77	3.17	0.008	0.005	0.004	0.003				
Verbenaceae	*Aegiphila sellowiana*	tree	Red	1.0	4.03	6.21	5.55	7.74	0.134	0.042	0.042	0.092	7.57	8.70	10.18	21.48
Verbenaceae	*Lantana lilacina*	herb	Lilic	1.0	2.79	2.91	6.45	6.93	0.132	0.010	0.010	0.122				
Winteraceae	*Drymis brasiliensis*	tree	Purple	5.0	2.00	3.98	6.40	8.55	0.225	0.026	0.006	0.198	6.60	13.79	15.52	11.20

Bicolored fruits are indicated by two-colour combinations; for the morphologically cicolored fruits the colors represent, respectively, the colour of the flesh part and the ccessory(ies) structure(s), followed by capital letters (in parentheses) that indicate to which structures the preceding colours refer to. a = aril, b = bracts, c = capsule, f = fruit, p = edicel.

CAPÍTULO 3

INFLUENCE OF SPATIAL AND TEMPORAL VARIATION OF FRUIT TRAITS ON THE ABUNDANCE OF FRUGIVOROUS BIRDS ON THE ATLANTIC FOREST, BRAZIL

INFLUENCE OF SPATIAL AND TEMPORAL VARIATION OF FRUIT TRAITS ON THE ABUNDANCE OF FRUGIVOROUS BIRDS ON THE ATLANTIC FOREST, BRAZIL

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ABSTRACT

The patterns of spatial and temporal variation in abundance and morphological and nutritional quality of fruits were compared with the variation in abundance of frugivorous birds in three habitats over a 12 months period in the Atlantic Forest of southeast Brazil. The results showed a high spatial heterogeneity among habitats associated with differences in plant species composition. The habitats also had an asynchronous temporal patterns of fruit abundance and significant difference on monthly means of morphological and nutritional traits of fruits over vertical strata and among habitats. At the landscape level, these patterns suggest that, as a whole, the mosaic of different habitats can be seen as a non-seasonal unit, where each individual patch have complementary fruiting phenology. These conditions should affect bird communities because they were characterized by dynamic systems with temporal fluctuation on abundance and bird species composition. Significant correlations between fruit variables and bird abundance suggest that some bird species move into or out of habitats according to more favorable fruit availability. These results may have important implications for tropical management and conservation.

***Key words*:** spatial heterogeneity, temporal variation, frugivore, bird, nutritional composition, morphology, fruit, feeding strategy, Atlantic Forest.

INTRODUCTION

Variation in fruit resource availability at connected habitats permits wide-ranging species to persist in the community along with fixed ranges because animals may move around within a local habitat mosaic according to more favorable resource availability (Van Schaik *et al.* 1993). Although these species are referred to as 'nomadic' or 'migratory', correlations between fruit abundance and local bird abundance (Levey 1988, Loiselle and Blake 1991) could result if such animals are philopatric when resources are abundant, but then wander to or search for more favorable habitats as resources decline, thus becoming distributed among habitats so that they appear to track local resource flushes (Leighton and Leighton 1983).

The nature of this phenological mosaic is poorly known, but according to Leighton and Leighton (1983), three possibilities may be considered. First, habitats may have complementary fruiting phenologies, being regularly out of phase with one another. It is easiest to imagine this connected to some gradient, like elevation, in which climatic cues for flowering are staggered in time, as may be the case for Costa Rica (Loiselle and Blake 1991). Second, some habitats may be relatively aseasonal in fruit production compared to habitats around, thereby providing a refuge from fruit scarcity (Foster 1980). Finally 'nomads' may search for and track fruit flushes that occur stochastically within the same or between different forest formations in function of the local variation in tree species composition within a habitat, that may lead to sites being out of phase with one another.

The identification of bird species that respond to periods of low fruit availability through emigration to more favorable habitats has profound implications for the design of national parks and wildlife preserves (Fleming *et al.* 1987). These frugivorous birds seem especially vulnerable to local extinction because they require continuous access to a complete range of complementary habitats (Terborgh and Winter 1980, Loiselle *et al.* 1988).

The Atlantic Forest of southeast Brazil presents an excellent system for this kind of investigation because it is formed by a mosaic of vegetation types of primary forests and forests with successional stages (natural and human disturbed) (Mantovani *et al.* 1990). Besides this, the Atlantic Forest is considered one of the most important ecosystems in relation to bird species diversity, as many species are endemic or threatened and with restricted distribution (Parker *et al.* 1996, Goerck 1997).

Although it is not usual in phenological studies, we measured morphological and nutritional traits of fruits in each habitat because birds differ on these criteria on fruit selection (Chapter 2). Then, counting only the number of fruit or fruiting trees is insufficient to measure fruit resource availability accurately without considering the traits of the fruit crop also. The features of fruit are a major point for some specialist birds with narrow niche breadth, that select fruits with specific morphological and/or nutritional traits (Chapter 2). These species should be more sensitive to variations on fruit abundance and features than generalist species that can shift their diet during periods of fruit scarcity.

In this paper we formulate the hypothesis that the mosaic of vegetation in the Atlantic Forest of southeast Brazil is important to maintain some set of frugivorous birds, causing asynchronization in the fruit phenology on different patches, that allows bird movements in response to local food scarcity. We might expect this kind of behavior for specialist bird species that select fruits on the basis of specific morphological and/or nutritional traits. On the other hand, the generalist birds should be less affected by local seasonal variation on fruit resource as their broad morphological and nutritional tolerance on fruit selection enable them to use a wide range of fruit types that are available in the habitat. Therefore, this study addresses the following questions:

1) How do the features and the abundance of fruits vary among the vegetation types in the understory and in the canopy?
2) What is the effect of temporal variation of the features and abundance of fruits in each type of vegetation and in different vertical stratification?
3) How does the frugivore bird community respond to this variation on fruit availability? Is there spatial and temporal differences in the number and composition of frugivorous bird captured? Is the number of birds captured correlated with fruit abundance or fruit features?

MATERIAL AND METHODS

STUDY AREA

The study was conducted in three Atlantic rain forest sites in the Parque Estadual Intervales (PEI) in southern São Paulo State, southeastern Brazil (Fig. 3. 1). The average annual rainfall is 1500 to 1800 mm and temperature is 17 to 19°C (SMA 2001). PEI is a 49,000 ha protected area surrounded by three other reserves encompassing a total of 120,000 ha of continuous forest. PEI is composed of different types of physiognomies along an altitudinal gradient from 60 to 1,100 m, with climate and soil also varying along this gradient (Mantovani 2001). The forest sites are different from each other and are characterized by hilltop, middle slope and bottom of valley (Mantovani *et al* 1990). The vegetation in these physiognomies is classified as Lower Montane Rain Forest (700-1,100 m a.s.l.), and is considered to be "typical" Atlantic Forest (Oliveira-Filho & Fontes 2000).

The hilltop (HT) is located at "Mirante da Anta" (24°16' 42''S and 48° 24' 28''W) at *ca* 1,000 m elevation. In function of the variation in soil depth, there are many types of forests in hilltop including forest similar to that found in the middle slope, field formation with treelets and shrubs or typical species of secondary forest. The middle slope (MS) is located at "Barra Grande" (24°18' 17''S and 48° 21' 53''W) at about 900 m elevation. The canopy is 15-20 m high. The bottom of valley (BV) is located at "Carmo" (24°18' 60''S and 48° 25' 00''W) at about 700 m elevation. The irregular canopy is 20 m high with emergent individuals up to 30 m. For a detailed description of vegetation at PEI see Mantovani *et al.* (1990).

We selected the localization of three study sites by vegetation type and topographic zone to cover the existing environmental variation. In each forest site five sample units were established for phenological data and as sites for mist nets (Fig. 3. 2). Nearest neighbor distance among the units of the same site varied from 10 m to 1,000 m and from 10,000m to 20,000 m between sites. Because much of the study areas were too topographically rugged to accommodate the mist nets or with limitation area, we were forced to choose sites based on an additional feasibility criterion. These units were determined a priori to produce an independent data set from each habitat type for statistical analyses.

PHENOLOGICAL DATA

Within units we established three plots of 10 x 25 m distributed along the line of mist net and distant 1 m off the line (Chapman *et al.* 1994). We sampled in the plots only the zoochorous plants that produce fleshy fruits and had ripe fruits, because they clearly correlated with frugivorous birds and influence their habitat selection (Loiselle and Blake

1991). We judged ripeness based on color changes, size and softness during maturation of fruits (Levey 1988). We used "fruits" in its ecological, and not botanical sense, to denote "functional fruits", i.e., packages made up of seeds plus accessory tissues used as food by birds, irrespective of their anatomical origin (Herrera 1992).

All the plots were monitored monthly during one year at the same time that birds were captured. The MS was sampled from April 1999 to March 2000, BV from April 2000 to March 2001 and HT from April 2001 to March 2002. The fruiting plants were counted, identified and individually marked.

Fruit abundance was evaluated counting all the fruits in the fruiting plants. We visually estimated the number of fruits in trees with large crowns and a great (more than 1,000 fruits) (Chapman *et al.* 1992, Shu-Yi and Li-Xin 1995). For estimation, 10% of the crown, exposed to full view, was chosen as a sample, and the fruits were counted therein, the number obtained being subsequently multiplied by 10.

Fruits of each species were collected for calculation of the fruit mass. The mean individual fruit weight of each species was estimated from approximately 10 fruits. The fruit production of each species was calculated by multiplying the fruit number by a mean individual fruit weight, and the total fruit production was obtained by adding the production of all plant species sampled (Shu-Yi and Li-Xin 1995). The fruit production measured was expressed as g/750 m^2 (total area sampled per unit = 3 plots x 10 m x 25 m).

We classified the fruiting plants in two categories according to the size of their largest diameter of seed (small < 5.0 mm and large ≥ 5.1 mm) in order to qualify the food available for birds. We chose the size of seed to define the category because this morphological trait was one limiting factor on fruit selection by birds (Chapter 2).

Furthermore, we measured the height of the trees and divided then into two vertical strata: canopy and understory. For BV and MS, the plants with less than 10 m were classified in the understory and more than 10 m in the canopy (Levey 1988). For HT we used 5 m as a height limit separate the plants between the understory and the canopy, because the maximum height of the trees was lower than the other study sites (Chapter 1).

MORPHOLOGICAL AND NUTRITIONAL CHARACTERIZATION OF FRUIT AVAILABILITY

Samples of ripe fruits were collected and the following morphological and nutritional data were obtained: total mass of fruit, seeds and pulp; largest and smallest diameter (length and width) of fruit and seed; number of seeds and percentage (%) of proteins, lipids, soluble sugar and insoluble sugar per gram of dry pulp. Measurements were taken from, at least, 10 fruits, chosen whenever possible from different individuals in fructification. Most of the collections were made on the ground beneath the parent trees or sometimes directly picked from trees with a branch-cutter. The chemical analyses were made in the Laboratório de Ecologia Química of Instituto de Biologia of Unicamp – Brazil. Protein was determined according to the methods described by Jeffery *et al.*, (1989), lipid by Bligh and Dyer (1959) and soluble and insoluble sugar by Fales (1951), Kearns and Inouye, (1993) and Poorter and Villar (1997).

The monthly crop feature for each unit was calculated by the average of morphological and nutritional traits of all fruiting plant in the unit. In this way, for each fruit trait, average was calculated adding the value of fruit trait of the specie the for all fruiting plants and the total obtained was divided by the number of individuals.

BIRD COMMUNITY

Although mist nests are known to introduce bias in estimates of bird community structure and dynamics (specially for canopy and less active species), we used this method because it provide identical sampling of different habitat and its accuracy is relatively independent of observer biases and skills (Levey 1988, Blake and Loiselle 2000, Pearman 2002).

Birds were captured in five units for each forest site (BV, MS, and HT) with 10 mist nets per unit (36 mm mesh, 12 x 2.5 m) distributed in five units. We placed the nets in line on these units and each unit were sampled one day each month during one year (total sampled 3,600 mist-net-hours per site). They were open from dawn to early afternoon (6 hours). We checked nets at least once per hour and more than this during rain.

All frugivorous birds were identified and banded with numbered aluminum leg bands. Species captured were assigned to distinct ecological groups (guild) based on feeding habitats, foraging substrate, and preferred foraging strata in the vegetation. This classification was based on Willis (1979), Allegrini (1997) and Aleixo (1999) into: large canopy frugivores (C-LF), edge frugivores/insectivores (E-FI), canopy frugivores/insectivores (C-FI) and edge omnivores/insectivores (E-OI) (Appendix 3. 1). Canopy species were included in the analyses because the units were topographically rugged and nets could also sample the canopy. Furthermore, most of bird canopy are not restricted to the canopy, they can be seen sometimes in the understory in function of the variation on resource availability among the vertical stratification.

Bird species were classified according to their feeding strategies and their preferential traits of fruit consumed based on Chapter 2. Following this chapter, bird species may have morphological and/or nutritional specialization with specific traits of fruit selection. We considered this selection on the correlation with each fruit mass category.

STATISTICAL ANALYSES

1) **Plant diversity and similarity among habitats** - We compared the three habitats in terms of fruiting plant species composition, diversity and similarity using the following indices: Shannon-Wiener (h'), Shannon evenness (E) and Sorensen quantitative (Magurran 1988).

2) **Spatial and seasonal variation on fruit abundance** - We compared the spatial and seasonal variation in fruit production using multivariate analysis of variance (MANOVA). We selected this test because we were interested in analyzing, at the same time, four dependent variables resulted from the stratification and seed size combinations (canopy - large seed, canopy - small seed, understory - large seed and understory - small seed). From this test, we obtained a multivariate F value (Wilks' lambda) based on a comparison of the error variance/covariance matrix and the effect variance/covariance matrix. The "covariance" here was included because the four measures were probably correlated and we must take this correlation into account when performing the significance test. In case of the overall multivariate test was significant, our next step was to look for a particular main effect or interaction of the dependent variables, trying to identify the specific dependent variables that contributed to the significant overall effect. In addition, we applied Tukey's HSD (Honest Significant Difference) where p-values indicated the *post hoc* significance levels for the respective pairs of means. We analyzed our data as repeated measures designs, where we had five independent data set units on fruit production compared for each one of the three sites

(BV, MS and HT). At the end, we compared the fruit production between strata for each fruit category and among habitats to evaluate the temporal similarity (i.e., parallel change in abundance), through phenological patterns of synchrony or asynchrony in fruit production using Spearman rank correlation.

3) **Spatial and seasonal variation in fruit feature** - The feature of fruit available to birds was measured by the monthly average of morphological and nutritional traits of all fruiting plants in each unit. The comparison among habitats and months were made using the same tests described for fruit abundance: Manova, Tukey HSD test and Spearman rank correlation. The dependent variables for morphological characterization were: total mass of fruit, seeds and pulp, largest and smallest diameter (length and width) of fruit and seed and number of seeds. For nutritional characterization we used these following variables: percentage (%) of proteins, lipids, soluble sugar and insoluble sugar.

4) **Spatial and seasonal variation in bird capture** – First of all, we compared the similarity between the three habitats in relation to the number of bird captured using Sorensen quantitative index (Magurran 1988) and then we analyzed the temporal and spatial differences on bird captured for guilds (C-LF, E-FI, C-FI, U-FI and E-OI), as well as for the most abundant species captured (*Chiroxiphia caudata, Habia rubica, Mionectes rufiventris, Platycichla flavipes, Schiffornis virescens, Trichothraupis melanops* and *Turdus albicollis*). The comparisons among physiognomies and months were made using Manova and Tukey HSD test, through which we obtained the synchrony or asynchrony pattern for bird captures among habitats using Spearman rank correlation.

5) Correlations between abundance and features of the fruits and number of bird captures – In order to evaluate the influence of fruit abundance variation in bird capture, we applied the Spearman rank correlation test to the total fruit mass produced in all units of the same site for each category in the month and the number of bird captured. We tested the correlation for guilds and main bird species captured. According to the feeding behavior (described on Chapter 2) of the main bird species we made the following specific correlations: (1) *Chiroxiphia caudata, Habia rubica, Mionectes rufiventris, Schiffornis virescens* and *Trichothraupis melanops* versus fruit mass with small seeds in the understory; (2) *Carpornis cucullatus* and *Platycichla flavipes* versus fruit mass with large seeds in the canopy and (3) *Turdus albicollis* versus fruit mass with large seeds in the understory. Furthermore, we made correlations for all eight species considering the vertical strata where the captures occurred and the total fruit mass produced in the habitat. All these statistical analysis were performed by Statistica Program (1993).

RESULTS

We record 80 fruiting plant species of 31 families. Most of these species occurred in only one site (62 species – 77.5%) (Appendix 3. 1). MS had the highest diversity and consequently more equitability (Table 3. 1). Similarity between habitats were very low, specially between HT and the other two. Only four species (5% of total plant species) were found in all habitats: *Geonoma* sp., *Didymopanax angustissimum, Mollinedia boracensis* and *Mollinedia floribunda*.

1) Variation in fruit features and abundance

The abundance of fruit mass varied among habitats (Fig. 3. 3 and Table 3. 2a and 3. 2b). Fruit abundance in BV was higher than in MS and HT, being the main difference due to the production of fruits with large seeds in the understory. Peaks in fruit production almost followed a sequential pattern from HT (Jan, Feb, Mar, Apr, May) to BV (May, Jun, Jul), to MS (Sep, Out, Nov). Seasonal variation in fruit abundance among habitats was not significant and the combination of these two variables was slightly significant. The evaluation of fruit production between strata for each fruit category showed a weak temporal synchrony for fruits with small seeds in understory and canopy (Spearman rank correlation, r=0.2186, p=0.0032). The other correlations were not significant (i.e. asynchronous phenology). The phenological patterns of fruit abundance for each category among habitats was also asynchronous (Spearman rank correlation, p>0.05).

The monthly averages of morphological fruit traits varied significantly among habitats, months and by the combination of these two variables (Fig. 3. 4 and 3. 5; Tables 3. 3a and 3. 3b). Most of the morphological fruit traits had significant effects on these variations, mainly the seed mass, that influenced on a spatial and temporal basis. BV had the largest average of fruit mass and fruit size, as well as seed mass and seed size, being the opposite verified for HT. Temporally, the main effect observed in morphological variation occurred on December and January, months that had the largest average of seed mass in relation to March and May.

The monthly average of pulp nutritional composition showed significant temporal and spatial variation, as well as the combination of these two variables (Fig. 3. 6, 3. 7 and 3. 8; Tables 3. 4a and 3. 4b). Percentage of lipid was an important variable that contributed simultaneously to the spatial and temporal variation among habitats. BV had the highest average of % of protein and insoluble sugar. Insoluble sugar significantly decreased from BV, HT to MS, while the % of lipid increased from HT, BV to MS. With regard to temporal variation, the main effect was on the % lipid that was significantly higher in February than in the other months and % of soluble sugar, that was higher in October than in December. The nutritional fruit traits showed no significant correlation among habitats (Spearman rank correlation, p>0.05).

2) Frugivorous birds

Bird community variation – We captured 567 frugivorous birds (42 species) belonging to 11 families in 10,800 mist-net-hours (Appendix 3. 2). Frugivorous accounted for 35% of all birds captured. Species composition differed among habitats, although similarity was higher than among fruiting plants. Eleven species (26% of total frugivorous species) were captured in all habitats (*Trogon rufus, Schiffornis virescens, Ilicura militaris, Chiroxiphia caudata, Mionectes rufiventris, Elaenia mesoleuca, Platycichla flavipes, Turdus albicollis, Basileuterus culicivorus, Euphonia pectoralis* and *Trichothraupis melanops*). MS and BV were the most similar sites in terms of bird capture, while BV and HT were the most different (Table 3. 5).

The number of bird capture within guilds varied significantly over time and among habitats (Fig. 3. 9; Tables 3. 6a and 3. 6b). The main effect were in the capture of C-LF, C-FI and U-FI. The guild U-FI had important contribution to the spatial and temporal variation in bird capture. Captures were higher in this guild in BV in April, June and September than in February and March, when contrasting MS and HT. U-FI was the only guild that showed a weak but significant temporal synchrony with BV and HT (Spearman rank correlation, r=0.596, p=0.040). C-LF and C-FI were less captured in MS in relation to the other habitats.

Correlation among frugivores and fruit abundance – In general, the high number of frugivores captured in BV coincided with the high average of fruit mass in the same habitat (Fig. 3. 3 and 3. 9). Fruit abundance was weakly correlated with three guilds but no correlation were found in MS (Table 3. 7). U-FI was correlated with fruits with large seeds in BV understory, total fruit understory and fruits with small seeds in HT understory. E-FI and E-OI were correlated with total fruit mass in HT (Table 3. 7).

Regarding the temporal variation in the average of fruit feature, we found significant but weak correlations with four guilds on MS and HT. Percentage of protein were negatively correlated with E-FI and E-OI and insoluble sugar positively correlated with C-FI in HT. In MS we found a positive correlation among soluble sugar and U-FI (Table 3. 7).

3) Bird species

Bird species variation - The evaluation of the eight bird species more frequently captured showed a significant difference among habitats, months and over time within each habitat (Fig. 3. 10; Table 3. 8a and 3. 8b). The main variation effect occurred in the capture of *Carpornis cucullatus, Habia rubica, Trichothraupis melanops* and *Turdus albicollis*. *Habia rubica* and *Trichothraupis melanops* were specially important because they affected simultaneously on spatial and temporal variation. Although these species were more captured in BV in June and August, the pattern of bird capture over time within each habitat showed temporal asynchrony among habitats (Spearman rank correlation, p>0.05).

Regarding the other species, *Carpornis cucullatus* was more captured in HT and *Turdus albicollis* was less captured in this same site.

Correlation among bird species and fruit abundance – We obtained weak but significant correlations for three bird species (*Chiroxiphia caudata, Habia rubica* and *Trichothraupis melanops*) (Table 3. 9). The stronger correlations were among *Habia rubica* and total fruit mass in BV understory, and among *Trichothraupis melanops* and fruit with small seeds in HT understory and the total understory biomass.

The temporal variation in the average fruit feature influenced the number of bird species captured with the exception of *Turdus albicollis,* but we did not find significant correlation among the pairs of variables in all habitats. Although significant, they were also weak. *Trichothraupis melanops* had more number of correlations in HT with % protein, insoluble and soluble sugars (Table 3. 9).

4) Consideration of feeding strategies

Following the Chapter 2 definition, all eight birds were characterized by a generalist diet with high plant species richness, nutritional flexibility and morphological specialization. With regard to morphological specialization, the larger birds (*Carpornis cucullatus, Platycichla flavipes* and *Turdus albicollis*) selected mainly fruits with large seeds. On the other hand, the smaller birds (*Chiroxiphia caudata, Habia rubica, Mionectes rufiventris, Schiffornis virescens* and *Trichothraupis melanops*) selected fruits with small seeds.

For these species we found three kinds of variation in the capture pattern: (1) no spatial and temporal variation: *Chiroxiphia caudata, Mionectes rufiventris* and *Schiffornis virescens;* (2) spatial variation only: *Carpornis cucullatus, Platycichla flavipes* and *Turdus* *albicollis;* (3) spatial and temporal variation: *Habia rubica* and *Trichothraupis melanops* (Table 3. 8 a and b).

According to what is expected for large birds, we should have captured more birds in BV than in other two habitats because the high abundance of fruits with large seeds. This pattern was not observed for any of the large birds (*Turdus albicollis, Carpornis cucullatus Platycichla flavipes*) (Table 3. 8b).

Although there was no significant spatial and temporal variation in fruit mass with small seeds, two bird species (*Trichothraupis melanops* and *Habia rubica*) showed spatial and temporal variation with asynchrony among habitats and also had correlation with fruit abundance and feature (Table 3. 8b).

DISCUSSION

A high spatial heterogeneity among habitats associated with differences in plant species composition and vegetation structure (Chapter 1) has been shown for other studies in the Atlantic Forest (Mantovani *et al.* 1990, Mantovani 2001), probably as a result of different conditions of soil types, topography, streams and light exposition that can affect the spatial distribution of plant species (Webb *et al.* 1999, Oliveira-Filho *et al.* 1998).

These conditions also promote differences in the distribution of frugivorous bird species among habitats, due mainly to differences on fruit availability (Loiselle and Blake 1991, Goerck 1997). In tropical forests elsewhere, changes in abundance and bird species composition among habitats have been explained by several factors, including elevational gradients (Goerck 1999), historical events (Pearson 1975), habitat specialization (Goerck 1997), predation (Thiollay 1999). In the study area at P. E. Intervales, a combination of such factors is paramount in explaining the presence or absence of different species among habitats (Goerck 1999).

1) Spatial variation in fruit abundance and features and their effect on the frugivore assemblage

Fruit abundance – In general, we found a notable decline in fruit abundance and a great temporal difference on peak of fruit production toward the hilltop (HT). When species were grouped according to seed size and vertical strata, the fruit abundance in each group varied intensely among habitats and over time in each habitat. Some studies also reported these phenological differences between large-seeded species and small-seeded species (Smythe 1970, Jackson 1981). The difference of pattern among the groups and habitats may be due to the abundance and species composition of plants in each habitat and the variation on synchronized fruiting pattern at the individual and species level (Sun *et al.* 1996). The main effect of this spatial variation occurred because the high abundance of fruits with large seeds in the understory on bottom of valley (BV). *Euterpe edulis,* that occurred only in BV, contributed most to this variation producing more than 57% of total fruit mass, what, consequently, affected the general pattern of fruiting phenology in BV. This habitat also showed greater seasonal fluctuation in fruit production than other habitats which offered a more relatively constant supply of fruits.

Fruit features - Morphological traits also varied significantly among habitats, however, plant species tended to form a downward gradient in fruit size, with larger fruits being more abundant in BV than in HT. Differences on morphological fruit traits along the elevation gradient were also found in southern Spain, but the gradient in fruit size was reversed (Herrera 1985).

Effect on bird community - The spatial variation in morphological fruit traits may influence bird species composition (Herrera 1985). In fact, one should expect that the higher abundance of fruits with large seeds would probably attract more large frugivorous birds with wider gapes in BV than in HT. This guild (C-LF), however, showed no significant differences between BV and HT. Method limitation in bird capture using mist nets might have underestimated C-LF sampled in BV, where there was a higher canopy than in HT, introducing a bias that would affect a more clear perception of the interaction between spatial variation of fruit size and gape width (Blake and Loiselle 2000).

2) Temporal variation in fruit abundance and nutritional traits and their effect on the frugivores assemblage

Fruit abundance - The three habitats studied showed an asynchronous temporal pattern of fruit abundance over vertical strata and among habitats. At the landscape level, this pattern suggests that, as a whole, the mosaic of different habitats can be seen as a non-seasonal unit, where each individual patch have complementary fruiting phenology. This environmental characteristic is very important because it promotes a continuous food supply for frugivorous birds. Evidence of non-seasonal fruiting pattern was documented for vertical stratification in the Atlantic forest (Develey and Peres 2000), as well as for neighboring habitats in Costa Rica (Levey 1988, Loiselle and Blake 1991) and for Atlantic forest types (Morellato *et al.* 1989, Morellato *et al.* 2000).

The non-seasonal pattern may occur on tropical forests influenced by a combination of abiotic and biotic factors. First of all, this pattern is documented specially for areas with a few seasonality in precipitation (Reich 1995). In such areas, several fruiting peaks of different importance may occur as a result of both variations in rainfall intensity within the rainy season and in the phenological responses of different growth forms (Jordano 1992).

Secondly, phenology pattern may be influenced by interspecific competition for pollinators or seed dispersers, an event that might select adaptations that minimizes phenological overlap with other plants, which may depend on the same animal vectors (Rathcke and Lacey 1985).

Fruit feature - Nutritional features of fruits varied spatial and temporally, and by combination of these two factors. These results show no general phenological pattern for nutritional traits regarding seasonal variation as found in European fleshy fruits by Herrera (1982). This non-seasonal variation in nutritional fruit content was consistent with other phenological studies (Johnson *et al.* 1985, Eriksson and Ehrlén 1991).

Effect on bird community - Spatial and temporal variation in fruit features and abundance probably influenced bird communities because birds from the same guilds showed different spatio-temporal patterns in the three habitats (Poulin *et al.* 1994). U-FI was more abundant in BV and was characterized by a strong seasonal variation in the number of captures. In contrast, C-LF and C-FI showed only spatial variation and E-FI and E-OI no variation at all. Our results suggest that guilds may employ different strategies to face fruit scarcity. Guilds with strong seasonal fluctuation in number of captures may be composed by birds (*e. g. Habia rubica, Trichothraupis melanops*) that move for other habitats (Gomes 2001). On the other hand guild with no seasonal variation are composed by species that change their diet for other plant structures with lower nutritive value, or increase the percentage of arthropods in their diet (Gomes 2001).

The temporal variation in nutritional features are very important because the nutritional demands of birds presumably vary according to season, life-cycle, residency status and availability of alternative insect food (Herrera 1982). If one habitat is considered, the nutritional fruit features did not vary seasonally to mach the seasonal demands of the birds, but considering all the habitats at same time they can provide birds requirement. The high protein content found in BV during spring and summer may favor protein requirements as birds are usually engaged in reproduction and growth during these seasons. On the other hand, the increase in lipid content in MS before winter coincide with the requirements of energy storage for thermoregulatory activities in winter. In summer, birds may be favored by the abundance juicy, low-reward fruits with high concentration of sugar and water in BV, because birds increase evaporate water loss resulting from the high temperatures and behavioral thermoregulatory mechanisms based on enhancement of evaporate cooling (Herrera 1982).

These ephemeral hotspot areas, based on fruit feature or abundance, may influence bird movements around and within a local mosaic habitat according to their specific food requirement (Herrera 1985). Correlation between bird capture and fruit abundance and nutritional content in the habitats were found in this study. The number of captures of *Trichothraupis melanops* was correlated with the abundance of fruit with small seed in the understory and with the variation in fruit content of protein and soluble and insoluble sugars in BV. *Habia rubica* showed correlation with total fruit mass in the understory and with protein content in BV. Others studies also documented this bird adaptation to temporal and spatial variation in fruit abundance (Wheelwright 1983, Loiselle and Blake 1991, Levey 1988).

3) Why is many times difficult to detect cause-effect relationships between frugivorous birds and seasonal variation in fruit abundance?

Although we found significant correlations between fruit abundance and frugivorous birds at the guild and bird species level, the correlations were not strong and were absent for some species (e.g. *Turdus albicollis*) and in some habitats (especially in MS). The lack of a marked correlation was also observed in other studies (Loiselle and Blake 1991, French 1992, Gomes 2001) and may be attributed to some non-mutually exclusive reasons:

Overall effect – In the study area many factors limit bird distribution and promote fluctuations in bird abundance and movements (Chapter1) and the food abundance and feature is just one of them. The perception of how food influence bird populations is made clear only under strong variation in the resource feature and abundance (Cody 1981, Pulliam and Dunning 1987). For example, we found correlation with bird species in habitats with the highest average of % protein, or in the lowest average of % lipid and protein.

Other adaptations for seasonal food scarcity including dietary switching – Bird species may employ several strategies to escape from food scarcity other than moving to other habitats. Species without fluctuation in abundance over time, as *Turdus albicollis,* may have the ability to supplement nutritional demands with insect or other plant structure with low nutritional value (fleshy petioles, nectar, leaves), or even with the chemical deterrents found in immature fruits (Van Shaik *et al.* 1993, Poulin *et al.* 1994, Galetti *et al.* 2000).

Species requiring mixed habitats – The lack of strong correlation may be associated to the opportunistic nature and the high tolerance of some bird species in moving between habitats (Fleming et al. 1987, Law and Dickman 1998). Time lags also complicate the picture, as individuals and populations may not respond immediately to changes in habitat features or abundance of resource, making fuzzy the relationship with these variables (Wiens 1989). Because of this complex behavior, it is sorely needed a more detail analyses of individual species over number of years that encompass different habitats for a full understanding of this behavioral pattern (Loiselle and Blake 1991).

4) Effect on specialist birds

From eight specialist birds linked to morphological fruit traits, only *Trichothraupis melanops* and *Habia rubica* showed spatio-temporal fluctuation on the number of captures, indicating that multiple patches of habitats are required in order to provide enough resources at the different stages of their life-cycle (Law and Dickman 1998).

Specialist bird populations, as *Carpornis cucullatus*, remained relatively stable over the study time, being probably favored by the extending of their foraging activities into different forest strata, as can be inferred from the asynchronous pattern of utilization between the canopy and the understory (Silva *et al.* 2002).

5) Conservation biology

The knowledge of multiple habitat use by birds has considerable practical value for land managers, as such knowledge can be incorporated into the design of fauna surveys. The appropriate habitat must be surveyed at the correct time or a species could be overlooked (Law and Dickman 1998). Because each species differ on both their home range sizes and particular resource requirements, the scale of the mosaics used by them vary. Our data stress the need for a careful consideration of the multifaceted aspects involving the habitat selection mechanisms of frugivorous birds species, which too often provide useful information for tropical management and conservation.

CONCLUSION

Spatial and temporal heterogeneity and complexity are critical elements in the function and stability of Atlantic Forest. Then it is important to conserve the processes that maintain such heterogeneity and complexity for bird communities preservation. Bird communities have dynamic equilibrium with temporal fluctuation on bird abundance species composition that, probably, are influenced by the temporal end spatial variation on food availability.

The results showed a high spatial heterogeneity among habitats associated with differences in plant species composition. The habitats also had an asynchronous temporal patterns of fruit abundance and significant difference on monthly means of morphological and nutritional traits of fruits over vertical strata and among habitats. At the landscape level, these patterns suggest that, as a whole, the mosaic of different habitats can be seen as a non-seasonal unit, where each individual patch have complementary fruiting phenology.

These conditions should affect bird communities because they were characterized by dynamic systems with temporal fluctuation on abundance and bird species composition. Significant correlations between fruit variables and bird abundance suggest that some bird species move into or out of habitats according to more favorable fruit availability. These results may have important implications for tropical management and conservation.

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LITERATURE CITED

ALEIXO, A. 1999. Effects of selective logging on a bird community in the Brazilian Atlantic forest. *Condor* 101(3): 537-548.

ALLEGRINI, M. F. 1997. *Avifauna como possível indicador biológico dos estádios de regeneração da Mata Atlântica*. MsC. Thesis. USP. 161 p.

BLAKE, J. G., and LOISELLE, B. A. 2000. Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. *Auk* 117 (3): 663-686.

BLIGH, E. G., and DYER,W. J. 1959 A rapid method of total lipid extraction and purification. *Can. J. Biochem. Physiol.* 37: 911-917.

CHAPMAN, C. A, CHAPMAN, L. J., WANGHAM, R., HUNT, K., GEBO, D., and GARDNER, L. 1992. Estimators of fruit abundance of tropical trees. *Biotropica* 24(4): 527-531.

CHAPMAN, C. A, WANGHAM, R., and CHAPMAN, L. J. 1994. Indices of habitat-wide fruit abundance in tropical forest. *Biotropica* 26(2): 160-171.

CODY, M. L. 1981. Habitat selection in birds: The roles of vegetation structure, competitors and productivity. *BioScience* 31: 107-113.

DEVELEY, P. F., and PERES, C. A. 2000. Resource seasonality and the structure of mixed species bird flocks in a coastal Atlantic forest of southeastern Brazil. *Journal of Tropical Ecology* 16: 33-53.

ERIKSSON, O., and EHRLÉN, J. 1991. Phenological variation in fruit characteristics in vertebrate-dispersed plants. *Oecologia* 86: 463-470.

FALES, F. W. 1951 The assimilation and degradation of carbohhydrates by yeast cells. *J. Biol. Chem.* 193: 113-124.

FLEMING, T. H., BREITWISCH, R., and WHITESIDES, G. H. 1987. Patterns of tropical vertebrate frugivore diversity. *Ann. Rev. Ecol. Syst.* 18: 91-109.

FOSTER, R. B. 1980. *Heterogeneity and disturbance in tropical vegetation.* Pp.75-92. *In*: Soulé, M. E. and Wilcox, B. A. (Eds.). Conservation Biology., Sinauer, Sunderland, Mass.

FRENCH, K.1992. Phenology of fleshy fruits in a wet sclerophyll forest in southeastern Australia: are birds an important influence? *Oecologia* 90: 366-373.

GALETTI, M., LAPS, R., and PIZO, M. A. 2000. Frugivory by Toucans (Ramphastidae) at two altitudes in the Atlantic Forest of Brazil. *Biotropica* 32(4b): 842-850.

GÖERCK, J. M. 1997. Patterns of rarity in the birds of Atlantic Forest of Brazil. *Conservation Biology* 11(1): 112-118.

GÖERCK, J. M. 1999. Distribution of birds along an elevational gradient in the Atlantic forest of Brazil: Implications for the conservation of endemic and endangered species. *Bird Conservation International* 9(3): 235-253.

GOMES, V. S. M. 2001. *Variação espaço-temporal de aves frugívoras no sub-bosque e chuva de sementes em um trecho de Mata Atlântica no Estado de São Paulo.* MsC. Thesis, University of Campinas, São Paulo, Brazil. 82p.

HERRERA, C. M. 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* 63: 773-785.

HERRERA, C. M. 1985. *Habitat-consumer: Interactions in frugivorous birds.* Pp. 341-365. *In:* Cody, M. L. (ed.) Habitat selection in birds (Physiological ecology). Academic Press Inc.

HERRERA, C. M. 1992. Interspecific variation in fruit shape allometry phylogeny and adaptation to dispersal agents. *Ecology* 73(5): 1832-1841.

JACKSON, J. F. 1981. Seed size as a correlate of temporal and spatial patterns of seed fall in a neotropical forest. *Biotropica* 13: 121-130.

JEFFERY, G. H., BASSETT, J., MENDAHAM, J, and DENNEY, R. C. 1989 *Vogel's Textbook of Quantitative Chemical Analysis.* 4th edition. London, Longman Group.

JOHNSON, R. A., WILLSON, M. F., and THOMPSON, J. N. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. *Ecology* 66(3): 819-827.

JORDANO, P. 1992. *Fruits and frugivory.* Pp. 105-153. *In:* Fenner, M. Seeds: The ecology of regeneration in plant communities. Oxon. CAB international.

KEARNS, C. A, and INOUYE, D. W. 1993 *Techniques for pollination biologists.* University Press of Colorado.

LAW, B. S., and DICKMAN, C. R. 1998. The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. *Biodiversity and Conservation* 7: 323-333.

LEIGHTON, M. and LEIGHTON, D. R. 1983. *Vertebrate responses to fruiting seasonality within a Bornean rain forest.* Pp. 181-196.*In:* Sutton, S. L., Whitmore, T. C. and Chadmuck, A. C. (Eds.) Tropical rain forest: Ecology and management Blackwell Sci. Publ. , London.

LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecological Monographs* 58(4): 251-269.

LOISELLE, B. A, and BLAKE, J. G. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72(1): 180-193.

LOISELLE, B. A, BLAKE, J. G., MOERMOND, T. C., and MASON, D. J. 1988. Low elevation record resplendent quetzals in Costa Rica. *J. Field Ornithol.* 60(1): 86-88.

MAGURRAN, A. E. 1988. *Ecological diversity and its measurement.* Croom Helm, London. 179p.

MANTOVANI, W. 2001 *A paisagem dinâmica.* Pp. 81-91. *In*: Leonel, C. Intervales. Fundação para a conservação e produção florestal do Estado de São Paulo. Secretaria de Estado do Meio Ambiente.

MANTOVANI, W., RODRIGUES, R. R., ROSSI, L., ROMANIUC-NETO, S., CATHARINO, E. L. M., and CORDEIRO, I. 1990 *A vegetação na Serra do Mar em Salesópolis, SP.* 1: 348-384. *In*: II Simpósio de Ecossistemas da Costa Sul e Sudeste Brasileira: estrutura, função e manejo. Academia de Ciências do Estado de São Paulo, Águas de Lindóia.

MORELLATO, L. P., RODRIGUES, R. R., LEITÃO-FILHO, H. F., and JOLY, C. A. 1989. Estudo comparativo da fenologia de espécies arbóreas de floresta de altitude e floresta mesófila semidecídua na Serra do Japí, Jundiaí, São Paulo. *Revista Brasileira de Botânica* 12: 85-98.

MORELLATO, L. P., TALORA, D. C., TAKAHASI, A., BENCKE, C. C., ROMERA, E. C. and ZIPPARRO, V. B. 2000. Phenology of Atlantic Rain Forest Tree: a comparative study. *Biotropica* 32(4b): 811-823.

OLIVEIRA-FILHO, A. T, and FONTES, M. A. L. 2000. Patterns of floristic differentiation among Atlantic forests in southeastern Brazil and the influence of climate. *Biotropica* 32(4b): 793-810.

OLIVEIRA-FILHO, A. T., CURI, N. VILELA, E. A., and CARVALHO, D. A. 1998. Effects of capony gaps, topography, and soils on the distribution of woody species in a Central Brazilian deciduous dry forest. *Biotropica* 30(3): 362-375.

PARKER, T. A. III, STOTZ, D. F., and FITZPATRICK, J. W. 1996. *Ecological and distributional databases*. Pp. 115-436. *In*: Stotz D. F., Fitzpatrick J. W., Parker T. A. III, and Moskovits D. K. (Eds.) Neotropical Birds: Ecology and conservation. University of Chicago Press, Chicago.

PEARMAN, P. B. 2002. The scale of community structure: Habitat variation and avian guilds in tropical forest understory. *Ecological Monographs* 72(1): 19-39.

PEARSON, D. L. 1975 The relation of foliage complexity to ecological diversity of three amazonian bird communities. *Condor* 77: 453-466.

POORTER, H., and VILLAR, R. 1997. *"The fate acquired carbon in plants: chemical composition and construction costs"*. *In*: Fakhri, A.; Bazzaz, J. G.. (Eds). Plant Resource and Allocation. Academic Press.

POULIN, B., LEFEBVRE, G., and MCNEIL, R. 1994. Characteristics of feeding guilds and variation in diets of birds species of three adjacent tropical sites. *Biotropica* 26(2): 187-197.

PULLIAM, H. R. and DUNNING Jr, J. B. 1987. The influence of food supply on local density and diversity of sparrows. *Ecology* 68: 1009-1014.

RATHCKE, B., and LACEY, E. P.1985. Phenological patterns of terrestrial plants. *Ann. Rev. Ecol. Syst.* 16: 179-214.

REICH, P. B. 1995. Phenology of tropical forests: patterns, causes, and consequences. *Can. J. Bot.* 73: 164-174.

SILVA, W. R., DE MARCO, P., HASUI, E. and GOMES, V. S. M. 2002. *Patterns of fruit-frugivore interactions in two Atlantic Forest bird communities of South-eastern Brazil: Implications for conservation,* Pp. 423-435. *In*: Levey, D. J., Silva, W. R. and Galetti, M. (Eds.) Seed dispersal and frugivory: ecology, evolution and conservation. Wallingford: CAB International.

SHU-YI, Z., LI-XIN, W. 1995. Comparison of three fruit census methods in French Guiana. *Journal of Tropical Ecology* 11: 281-294.

SMA 2001. *Intervales. São Paulo*: Secretaria do Estado do Meio Ambiente. 240p.

SMYTHE, N. 1970. Relationship between fruiting seasons and seed dispersal methods in a neotropical forest. *American Naturalist* 104(935): 25-35.

STATISTICA. 1993. *Statistica for windows*. Release 4.2. Statsoft, Inc.

SUN, C., KAPLIN, B. A., KRISTENSEN, K. A., MUNYALIGOGA, V., MVUKIYUWAMI, J., KAJONDO, K. K., and MOERMOND, T. C. 1996. Tree phenology in a tropical montane forest in Rwanda. *Biotropica* 28(4b): 668-681.

TERBORGH, J., and WINTER, B. 1980. *Some causes of extinction.*,pp.119-134. *In:* Soulé, M. E. and Wilcox, B. A. (Eds.) Conservation Biology Sinauer, Sunderland, Mass.

THIOLLAY, J-M. 1999. Frequency of mixed species flocking in tropical forest birds and correlates of predation risk: An intertropical comparison. *Journal of Avian Biology.* 30(3): 282-294.

VAN SCHAIK, C. P., TERBORGH, J. W. WRIGHT, S. J. 1993. The phenology of tropical forests: Adaptive significance and consequences of primary consumers. *Ann. Rev. Ecol. Syst.* 24: 353-377.

WEBB, E. L., STANFIELD, B. J., and JENSEN, M. L. 1999. Effects of topography on rainforest tree community structure and diversity in American Samoa, and implications for frugivore and nectarivore populations. *Journal of Biogeography* 26: 887-897.

WHEELWRIGHT, N. T. 1983. Fruits and the ecology of the resplendent quetzals. *Auk* 100: 286-301.

WIENS, J. A. 1989. *The ecology of bird communities.* Vol. 1. Foundations and patterns. Cambridges University Press, Cambridge. 539p.

WILLIS, E. O. 1979. The composition of avian communities in remanescent woodlots in Southern Brazil. *Papéis Avulsos de Zoologia* 33 (1): 1-25.

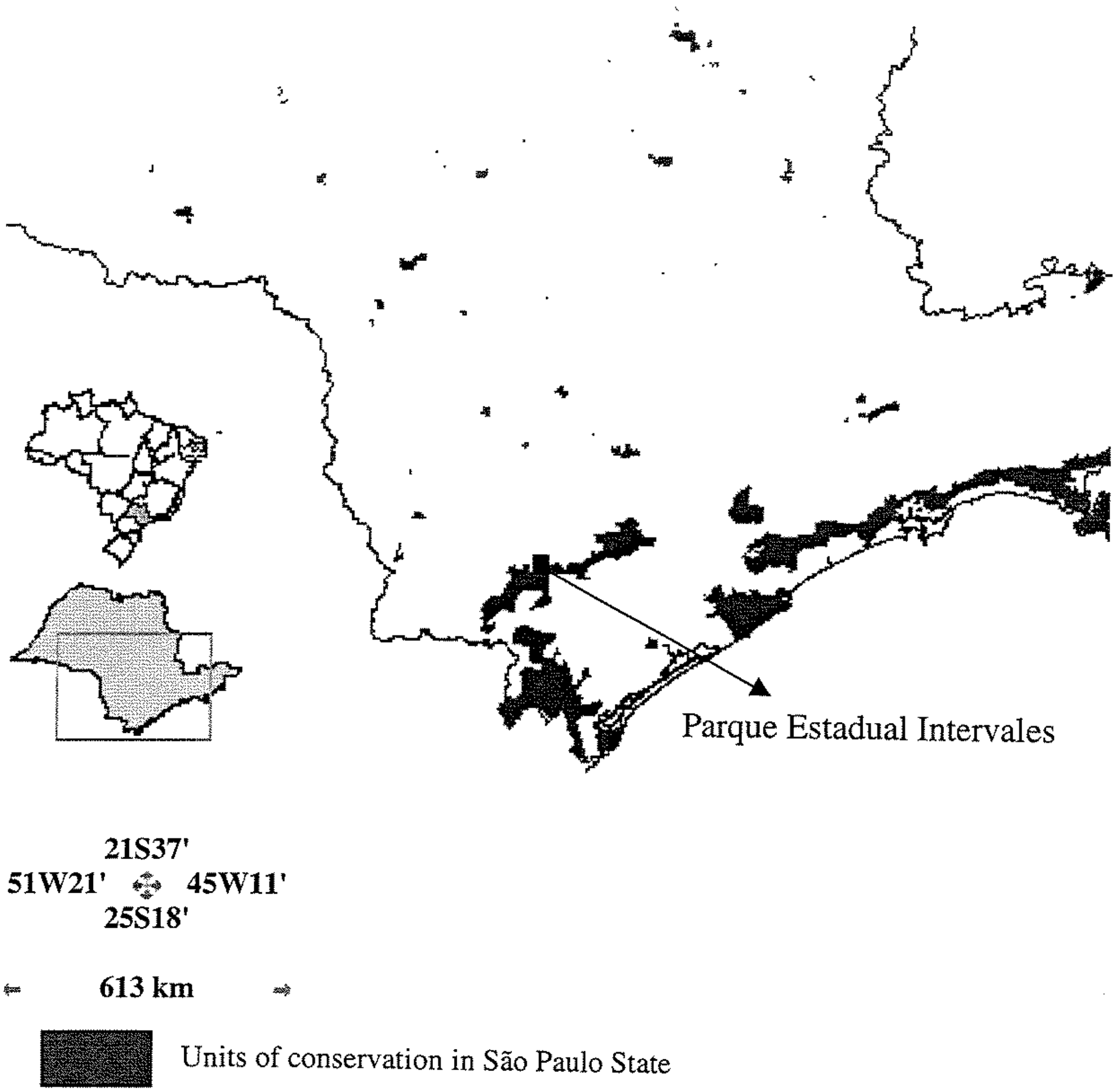

Fig. 3. 1. Localization of Parque Estadual Intervales in southern São Paulo State.

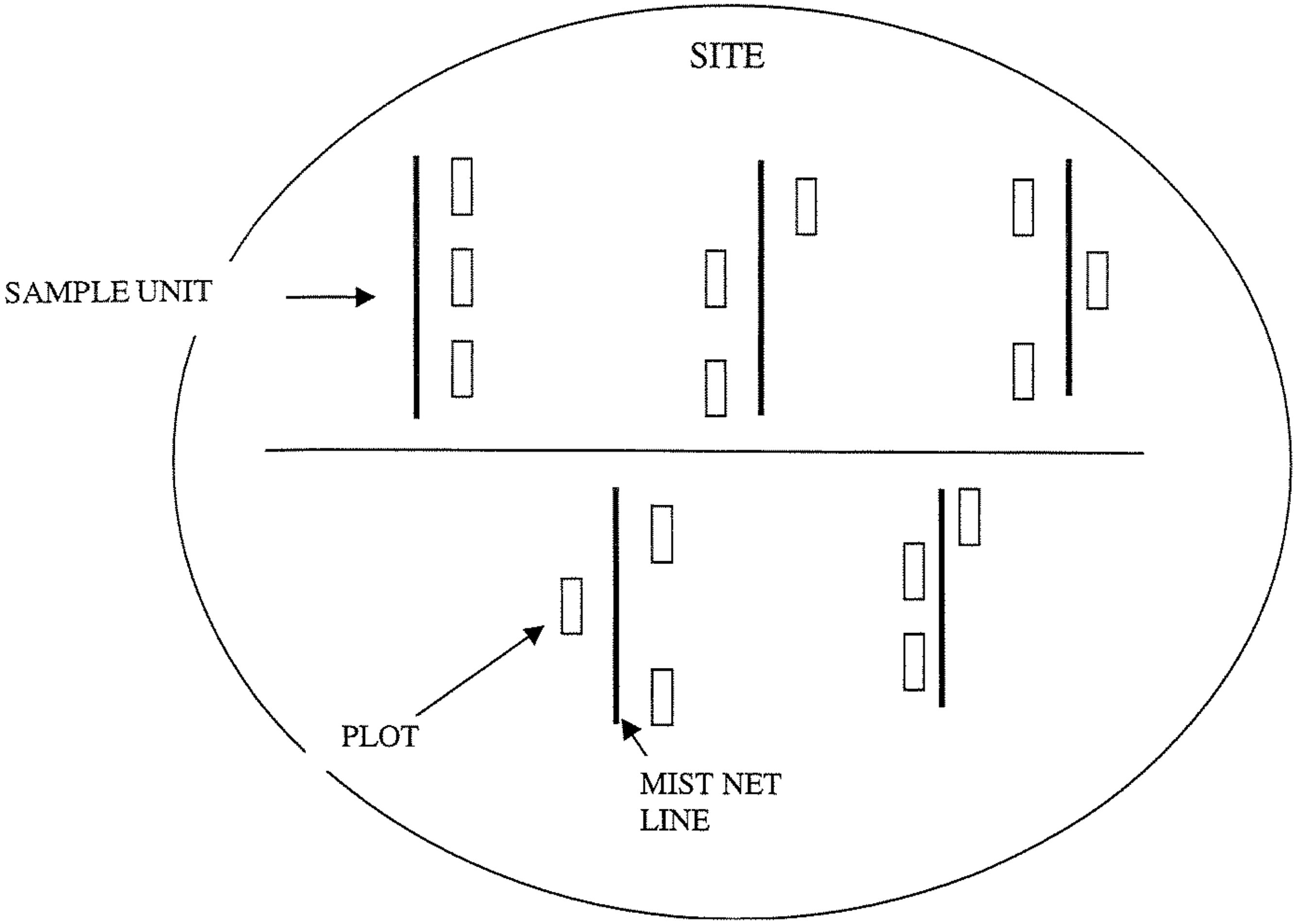

Fig.3. 2 Experimental design for each study site.

Table 3. 1. Comparative species richness and indices of diversity, evenness and similarity of fruiting plant species sampled in three different habitats: Bottom of valley (BV), Middle slope (MS) and Hilltop (HT) in Parque Estadual Intervales in southern São Paulo State.

	BV	**MS**	**HT**
Species richness (S)	33	31	37
Total number of sampled individuals	230	165	492
Shannon index of diversity (h')	2.094	2.678	1.994
Shannon evenness (E)	0.594	0.780	0.552
Sorensen index – quantitative data (Cn)			
BV		0.091	0.028
MS			0.088

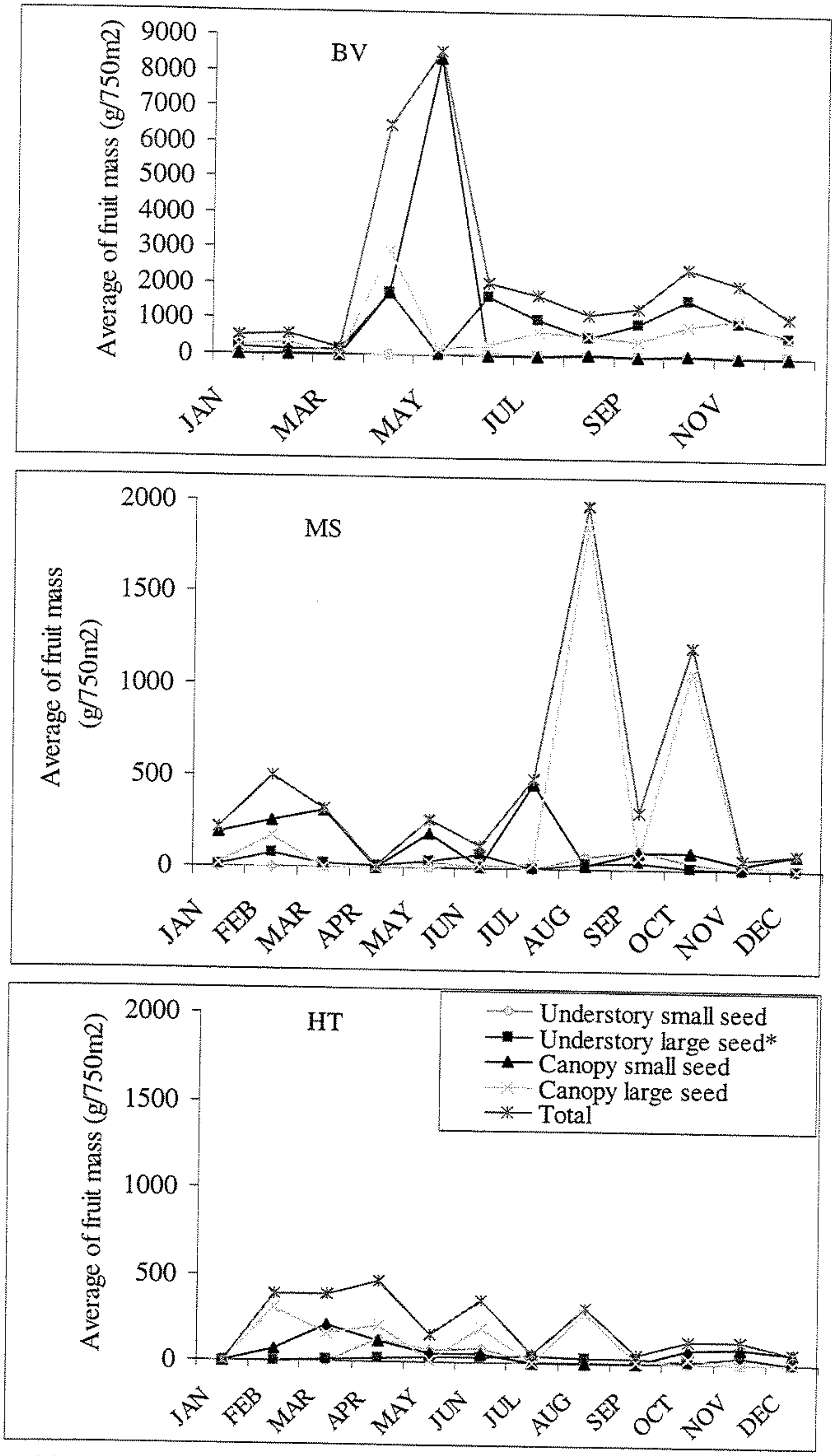

Fig. 3. 3. Means of fruit production within the understory and canopy with two categories of fruits (fruits with small seeds and fruits with large seeds) in three different habitats: Bottom of valley (BV), Middle

slope (MS) and Hilltop (HT) in Parque Estadual Intervales in southern São Paulo State. * significant difference in fruit mass among physiognomies (Manova p<0.0001 and Tukey p<0.0001 where BV>HT=MS).

Table 3. 2a. Manova analyis of variance considering two factors (type of physiognomy and months) and four dependent variables (two strata and two categories of fruit) in relation to fruit mass.

Manova: factors: physiognomy and month; variables biomass of fruit					
	Wilks'Lambda	**Rao's R**	**df 1**	**df 2**	**p-level**
Physionomy	0.6720	7.7492	8.0000	282.0000	**<0.0001**
Month	0.7229	1.0890	44.0000	541.0000	0.3258
Physiognomy x month	0.4915	1.2522	88.0000	560.0000	0.0718

Table 3. 2b. Specific effect on the physiognomic difference and Tukey HSD test showing the significant (p<0.05) differences between physiognomies and months.

		specific effect F(df1,2)		**Tukey (p<0.05)**
Strata	**Seed size**	**2,144**	**p-level**	**Physiognomy**
Undestory	Small	0.2722	0.7621	-
Undestory	Large	26.2554	**<0.0001**	BV>MS=HT
Canopy	Smalll	1.1026	0.3348	-
Canopy	Large	2.6869	0.0715	-

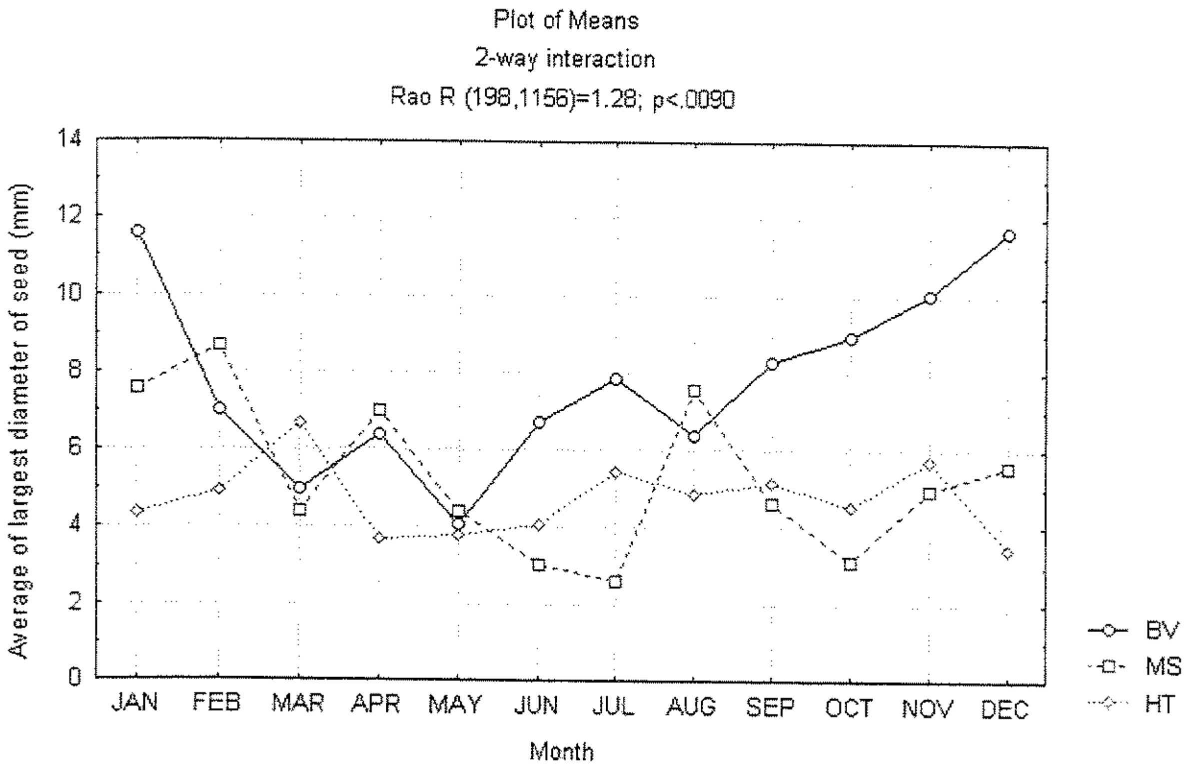

Fig. 3. 4. Averages of largest diameter of seed in three different habitats: Bottom of valley (BV), Middle slope (MS) and Hilltop (HT) in Parque Estadual Intervales in southern São Paulo State.

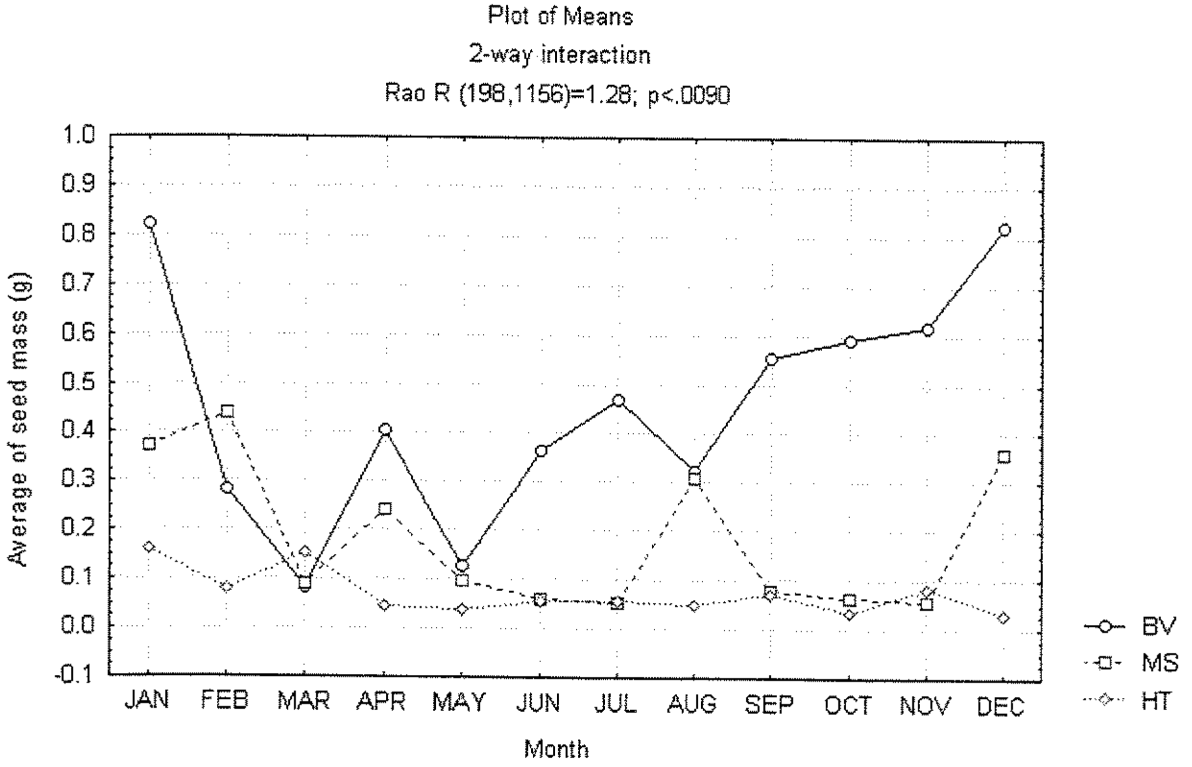

Fig. 3. 5. Averages of seed mass in three different habitats: Bottom of valley (BV), Middle slope (MS) and Hilltop (HT) in Parque Estadual Intervales in southern São Paulo State.

Table 3. 3a. Manova analysis of variance considering two factors (physiognomy and month) and nine dependent variables (average of morphological fruit traits)

Manova: factors: physiognomy and month; morphology of fruit					
	Wilks'Lambda	**Rao's R**	**df 1**	**df 2**	**p-level**
Physionomy	0.3743	9.5890	18	272	**2.026E-20**
Month	0.3018	1.8154	99	970	**6.185E-06**
Physiognomy x month	0.1905	1.2807	198	1156	**8.996E-03**

Table 3. 3b. Main effects variance in physiognomic factor considering the nine dependent variables (morphological traits) and Tukey HSD test showing the significant (p<0.05) differences between physiognomies and months.

	Main effect F(df1,2)		**Tukey HSDF (P<0.05)**	
	2,144	**p-level**	**physiognomy**	**month**
Fruit mass	8.6439	**0.0003**	BV>MS=HT	-
Seed mass	35.7070	**<0.0001**	BV>MS>HT	jan>mar=may and dec>may
Pulp mass	1.7207	0.1826	-	-
> fruit diameter	7.9177	**0.0005**	BV>MS=HT	-
< fruit diameter	11.1729	**<0.0001**	BV>MS=HT	-
Seed number	0.8422	0.4329	-	-
One seed mass	35.8607	**<0.0001**	BV>MS=HT	jan=dec>mar=may
> seed diameter	11.3359	**<0.0001**	BV>MS=HT	-
< seed diameter	20.0631	**<0.0001**	BV>MS=HT	-

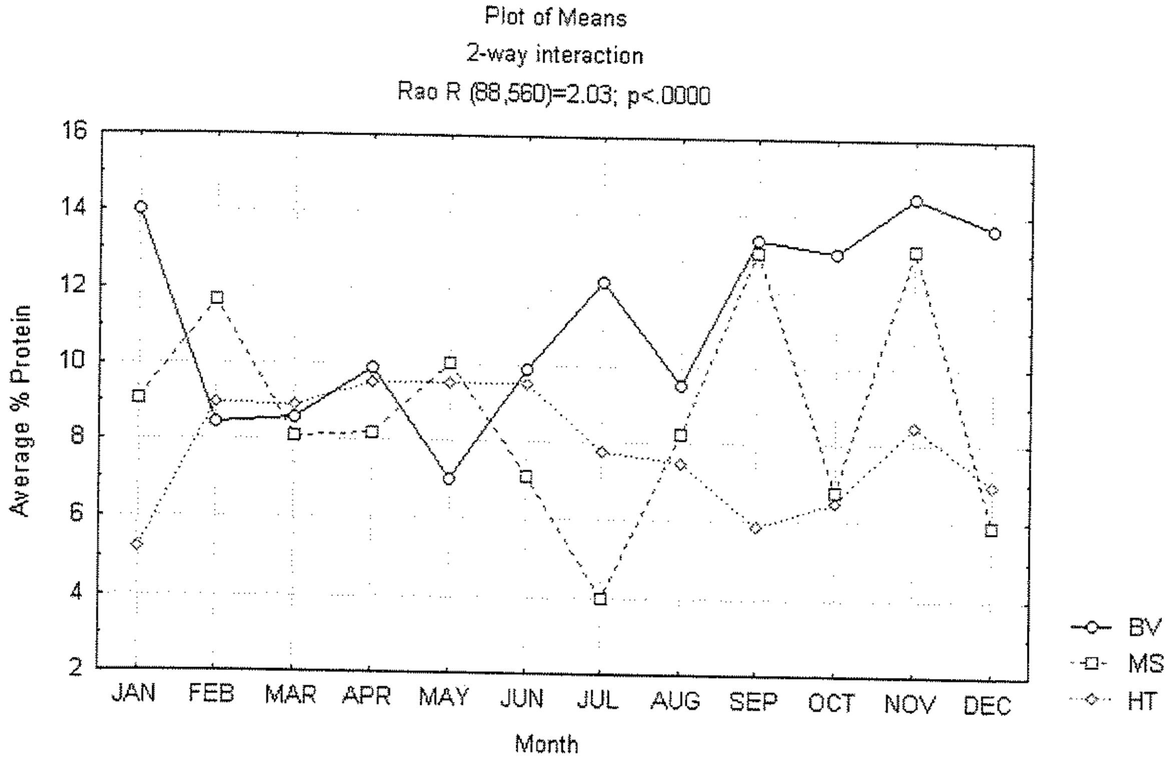

Fig. 3. 6. Averages of % protein in pulp of ripe fruits in three different habitats: Bottom of valley (BV), Middle slope (MS) and Hilltop (HT) in Parque Estadual Intervales in southern São Paulo State.

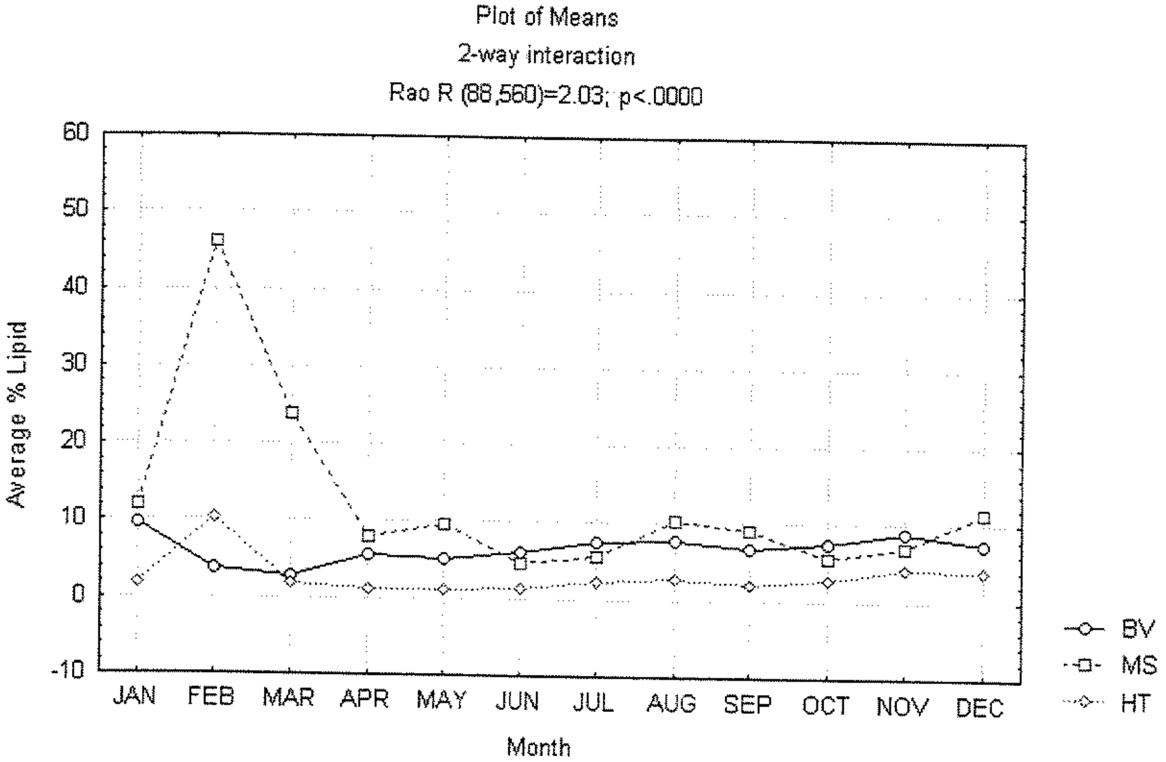

Fig.3. 7. Averages of % lipid in pulp of ripe fruits in three different habitats: Bottom of valley (BV), Middle slope (MS) and Hilltop (HT) in Parque Estadual Intervales in southern São Paulo State.

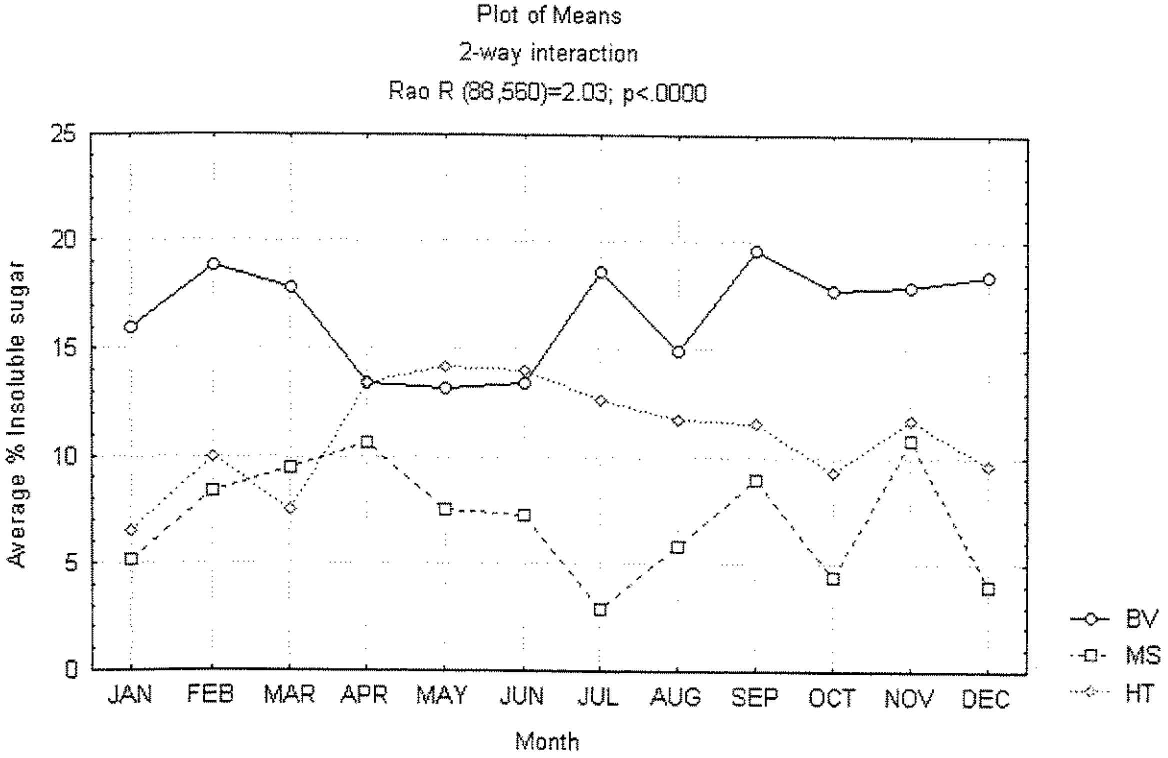

Fig. 3. 8. Averages of % insoluble sugar in pulp of ripe fruits in three different habitats: Bottom of valley (BV), Middle slope (MS) and Hilltop (HT) in Parque Estadual Intervales in southern São Paulo State.

Table 3. 4a. Manova variance analysis considering two factors (physiognomy and month) with four dependent variables (average of nutritional composition of fruits)

Manova: factors: physiognomy and month; nutritional compostion of fruit					
	Wilks'Lambda	**Rao's R**	**df 1**	**df 2**	**p-level**
Physionomy	0.3864	21.4560	8	282	**2.111E-25**
Month	0.5549	2.0480	44	541	**1.363E-04**
Physiognomy x month	0.3338	2.0348	88	560	**8.033E-07**

Table 3. 4b. Main effect of physiognomic factor variance for four variables (average of nutritional composition of fruits) and Tukey HSD test showing the significant (p<0.05) differences between physiognomies and months.

Main effect	**F(df1,2)**		**Tukey HSD (P<0.05)**	
	2,144	**p-level**	**physiognomy**	**month**
%Protein	9.3090	**0.0002**	BV>MS=HT	-
%Lipid	23.1594	**<0.0001**	MS>BV>HT	feb>all months
%Soluble sugar	1.0423	0.3553	-	oct>dec
%Insoluble sugar	55.3464	**<0.0001**	BV>HT>MS	-

Table 3. 5. Species richness and similarity index (Sorensen) for number of individuals birds captured in three different habitats: Bottom of valley (BV), Middle slope (MS) and Hilltop (HT) in Parque Estadual Intervales in southern São Paulo State.

	BV	**MS**	**HT**
Species richness (S)	21	19	35
Number of individuals	200	89	122
Number of captures	270	127	170
Sorensen index - quantitative data (Cn)			
BV		0.50	0.30
MS			0.36

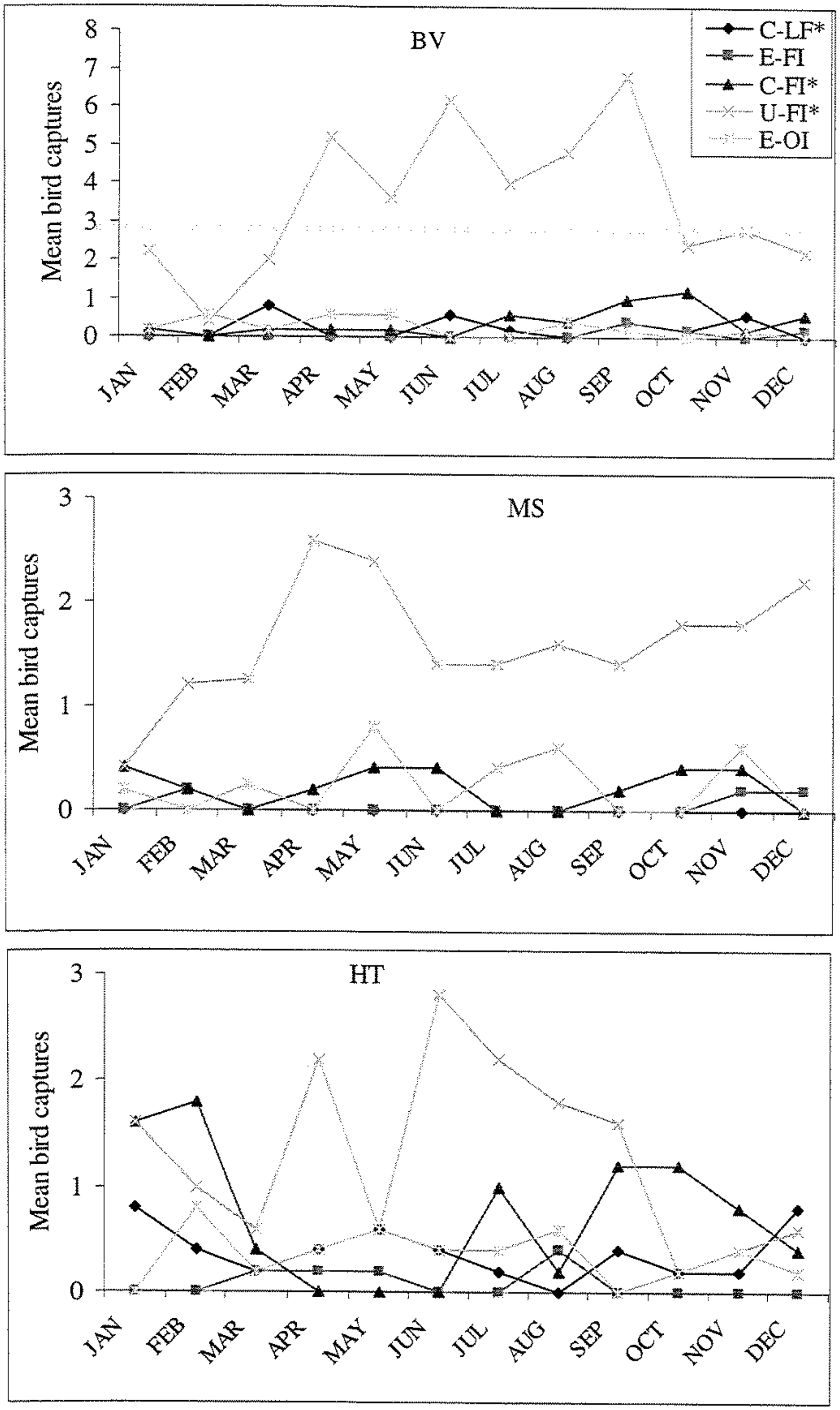

Fig. 3. 9. Average of large canopy frugivores (C-LF), edge frugivores/insectivores (E-FI), canopy frugivores/insectivores (C-FI), understory frugivores/insectivores (U-FI) and edge omnivores/insetivores

(E-OI) captured in three different habitats: Bottom of valley (BV), Middle slope (MS) and Hilltop (HT) in Parque Estadual Intervales in southern São Paulo State. * significant difference in bird captures among physiognomies and month (Manova $p<0.0001$ and Tukey $p<0.0001$).

Table 3. 6a. Manova analysis of variance considering two factors (physiognomy and month) with five dependent variables (number of bird captures clusterd in their guild)

Manova: factors: physiognomy and month; bird guild					
	Wilks'Lambda	**Rao's R**	**df 1**	**df 2**	**p-level**
Physiognomy	0.59908	8.17545	10	280	**1.3E-11**
Month	0.51225	1.84207	55	651	**0.00033**
Physiognomy x month	0.437	1.15587	110	690	0.147

Table 3. 6b. Main effect of physiognomic factor variance for six variables (number of bird captured clustered in their guild) and Tukey HSD test showing the significant ($p<0.05$) differences between physiognomies and months.

Main effect	**F(df1,2)**		**Tukey HSD (P<0.05)**	
Guild	**2,144**	**p-level**	**physiognomy**	**month**
C-LF	5.6899	**0.0042**	BV=HT>MS	-
E-FI	0.2222	0.8010	-	-
C-FI	3.8820	**0.0228**	BV=HT>MS	-
U-FI	29.5761	**<0.0001**	BV>MS=HT	apr=jun=sep>feb=mar
E-OI	0.6099	0.5448	-	-

Table 3. 7. Correlation coefficients (r) of Spearman rank correlation with $P < 0.05$ between bird captures within guilds and measures of fruit abundance and morphological and nutritional traits. N=12 .

	Habitat	**C-LF**	**E-FI**	**C-FI**	**U-FI**	**E-OI**
Morphological traits						
Understory large seed	BV				0.57	
Total understory biomass	BV				0.57	
Understory small seed	HT				0.56	
Total biomass	HT		0.58			0.58
Nutritional traits						
%soluble sugar	MS				-0.57	
% protein	HT		-0.60			-0.66
%insoluble sugar	HT			0.73		

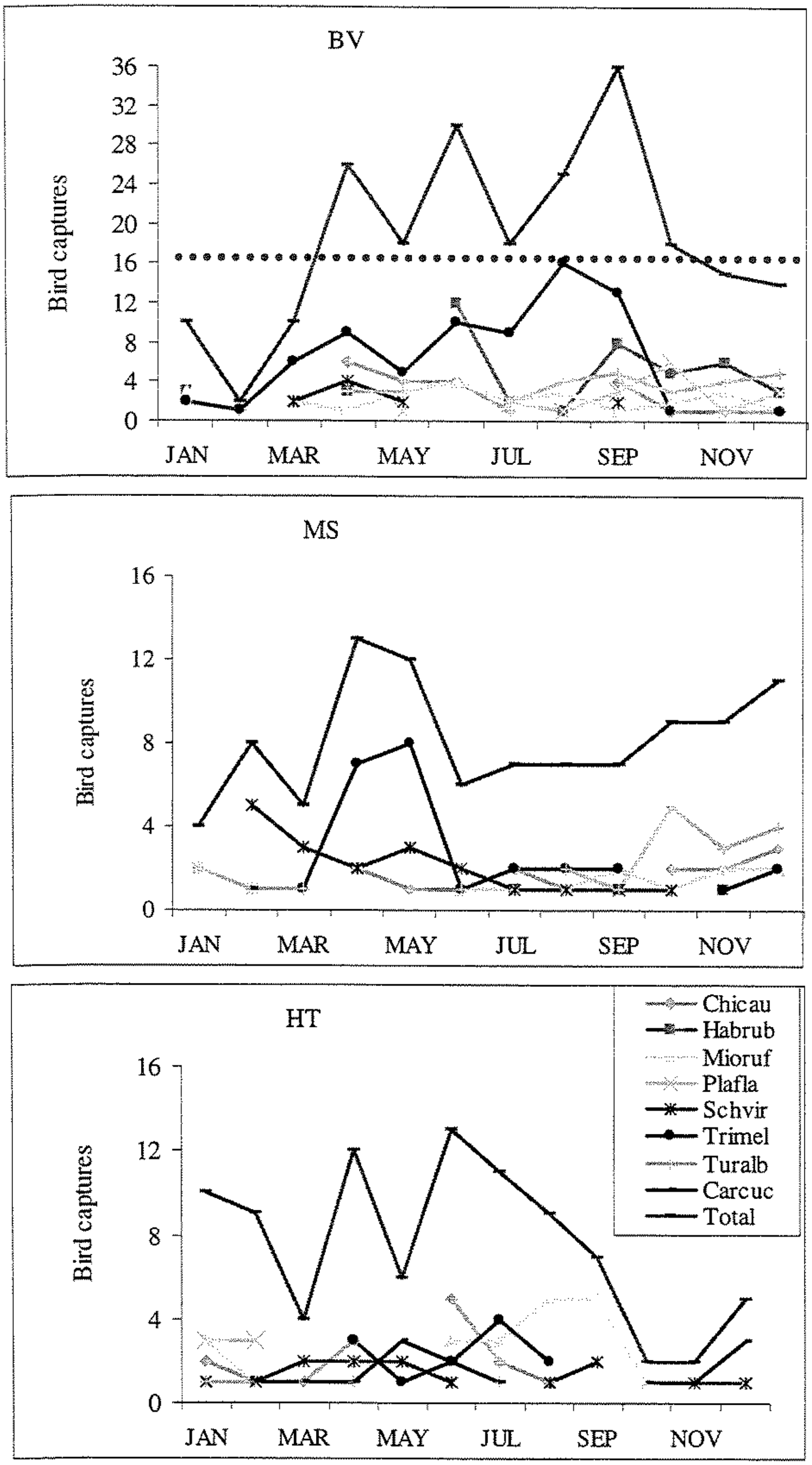

Fig. 3. 10. Number of bird captures in three different habitats: Bottom of valley (BV), Middle slope (MS) and Hilltop (HT) in Parque Estadual Intervales in southern São Paulo State. Species abbreviation as in Tab.3. 10

Table 3. 8a. Manova analysis of variance considering two factors (physiognomy and month) with eight dependent variables (number of captures for eight bird species)

Manova: factors: physiognomy and month; bird species					
	Wilks'Lambda	**Rao's R**	**df 1**	**df 2**	**p-level**
Physiognomy	0.4990	7.1174	16	274	**9.8125E-14**
Month	0.3453	1.8163	88	907	**1.7120E-05**
Physiognomy x month	0.2286	1.2870	176	1049	**0.0112**

Table 3. 8b. Main effect of physiognomic factor variance for eight variables (number of bird captures clustered in their species) and Tukey HSD test showing the significant (p<0.05) differences between physiognomies and months.

	F(df1,2)		**Tukey HSD (p<0.05)**	
MAIN EFFECT:	**2,144**	**p-level**	**Physiognomy**	**Month**
Carpornis cucullatus	8.5116	**0.0003**	HT>BV=MS	
Chiroxiphia caudata	1.6818	0.1897	-	
Habia rubica	23.3649	**<0.0001**	BV>MS=HT	jun>feb=mar=may
Mionectes rufiventris	1.4811	0.2308	-	
Platycichla flavipes	3.9277	0.0218	BV=HT>MS	
Schiffornis virescens	1.6267	0.2002	-	
Trichothraupis melanops	18.1702	**<0.0001**	BV>MS=HT	aug>jan=feb=oct=nov and may>oct=nov
Turdus albicollis	8.1525	**0.0004**	BV=MS>HT	

Table 3. 9. Correlation coefficients (r) of Spearman rank correlation with P<0.05 (*) and P<0.01 (**) between bird captures and measures of fruit abundance and morphological and nutritional traits. N =12.

	Habitat	**Ccucu.**	**Ccaud.**	**Hrubi.**	**Mrufi.**	**Pflav.**	**Svire.**	**Tmela.**	**Talbi.**
Morphological tracts	BV								
Understory small seed	BV								-0.68*
Understory large seed	BV			0.73**					
Total understory biomass	BV			0.73**					
Understory large seed	MS		-0.68*				0.68*		
Total understory biomass	MS		-0.61*						
Understory small seed	HT							0.74**	
Total understory biomass	HT							0.65*	
Nutritional tracts									
% protein	BV			0.69*					
% lipid	BV						-0.60*		
% soluble sugar	BV		-0.63*	-0.67*					
% insoluble sugar	BV				-0.66*				
% lipid	MS					0.57*			
% protein	HT	0.57*						0.58*	
% soluble sugar	HT							0.64*	
% insoluble sugar	HT							0.70*	

Species abbreviations: *Carpornis cucullatus* (Carcuc), *Chiroxiphia caudata* (Chicau), *Habia rubica* (Habrub), *Mionectes rufiventris* (Mioruf), *Platycichla flavipes* (Plafla), *Schiffornis virescens* (Schvir), *Trichothraupis melanops* (Trimel), *Turdus albicollis* (Turalb).

Appendix 3. 1. Number of fruiting plant species sampled in three different habitats: Bottom of valley (BV), Middle slope (MS) and Hilltop (HT) in Parque Estadual Intervales in southern São Paulo State.

Family	**Specie**	**BV**	**MS**	**HT**
Annonaceae	*Guatteria dusenii*	1	7	
Annonaceae	*Xylopia brasiliensis*	8		
Aquifoliaceae	*Ilex brevicuspis*		1	
Aquifoliaceae	*Ilex microdonta*			3
Aquifoliaceae	*Ilex pseudobuxes*			4
Araceae	*Euterpe edulis*	111		
Araceae	*Geonoma gamiova*		5	
Araceae	*Geonoma* sp.	1	21	35
Araliaceae	*Didymopanax angustissimum*	2	1	1
Bignoniaceae	*Anemopaegnea* sp.	1		
Cactaceae	*Rhipsalis campos portuana*	2		
Cactaceae	*Rhipsalis eliptica*	1		
Celastraceae	*Maytenus litoralis*	1		
Celastraceae	*Maytenus robusta*		5	
Clethraceae	*Clethra scabra*			2
Clusiaceae	*Clusia criuva*			3
Commelinaceae	*Dichorisandra tyrsiflora*		3	
Commelinaceae	*Tradescantia* sp.		6	
Ericaceae	*Leucothoe uleana*			1
Euphorbiaceae	*Alchornea triplinervia*		13	
Lauraceae	*Aniba firmula*			1
Lauraceae	*Ocotea aeciphila*		10	
Lauraceae	*Ocotea catharinensis*		1	
Lauraceae	*Ocotea puberula*	1		
Lauraceae	*Ocotea teleiandra*	3	7	
Leg. Mimosoideae	*Inga striata*			1
Liliaceae	*Smilax elastica*			1
Loranthaceae	*Psittacanthus* sp.	1		
Loranthaceae	*Struthanthus vulgaris*			2
Marcgraviaceae	*Marcgravia polyanthes*		2	
Melastomataceae	*Leandra cf. laevigata*		1	
Melastomataceae	*Leandra cordifolia*		2	
Melastomataceae	*Leandra dasytricha*	2		4
Melastomataceae	*Leandra melastomatoides*			4
Melastomataceae	*Leandra pilonensis*	2		
Melastomataceae	*Leandra* sp2			7
Melastomataceae	*Miconia budlejoides*			13
Melastomataceae	*Miconia cf. doriana*	4	3	
Melastomataceae	*Miconia cinnamomifolia*	2		
Melastomataceae	*Miconia inconspicua*	2		1

Family	**Specie**	**BV**	**MS**	**HT**
Melastomataceae	*Miconia pusilliflora*		50	
Meliaceae	*Cabralea canjerana*		2	2
Monimiaceae	*Mollinedia af. uleana*	2		
Monimiaceae	*Mollinedia boracensis*	1	1	5
Monimiaceae	*Mollinedia floribunda*	1	2	1
Moraceae	*Ficus luschnatiana*		1	
Myrsinaceae	*Ardisia guyanensis*	2		
Myrsinaceae	*Cybianthus peruvianus*			19
Myrsinaceae	*Myrsine coriacea*			1
Myrsinaceae	*Myrsine gardneriana*			50
Myrsinaceae	*Myrsine intermedia*			1
Myrsinaceae	*Myrsine umbellata*			4
Myrtaceae	*Calycorectes australis*	3		
Myrtaceae	*Gomidesia affinis*		2	29
Myrtaceae	*Marlierea eugeniopsoides*	3		
Myrtaceae	*Myrcia fallax*			5
Myrtaceae	*Myrcia grandiflora*	4	4	
Myrtaceae	*Myrcia rufala*		1	
Myrtaceae	*Myrtaceae indeterm.*			2
Myrtaceae	*Neomitranthes glomerata*			1
Myrtaceae	*Siphoneugena densiflora*		1	
Myrtacee	*Plinia plicato-costata*			1
Nyctaginaceae	*Guapira opposita*		4	
Ochnaceae	*Ouratea vaccinioides*			8
Olacaceae	*Tetrastylidium grandiflorum*	2		
Rubiaceae	*Alibertia mycifolia*		1	
Rubiaceae	*Amaioua intermedia*	4		
Rubiaceae	*Chamelia catharinae*	1	2	
Rubiaceae	*Psychotria forsterosnoides*			1
Rubiaceae	*Psychotria leiocarpa*	26		
Rubiaceae	*Psychotria longipes*		2	1
Rubiaceae	*Psychotria suterella*	31		3
Rubiaceae	*Psychotria vellosiana*			261
Rubiaceae	*Rudgea jasminoides*	2	1	
Sapindaceae	*Allophyllus edulis*	1		
Sapindaceae	*Cupania vernalis*	1	3	
Sapindaceae	*Matayba cf. juglandifolia*			1
Symplocaceae	*Symplocos glanduloso-marginata*			9
Urticaceae	*Urera baccifera*	1		
Winteraceae	*Drymis brasiliensis*			4
Total	*80*	230 (33 sp)	165 (31 sp)	492(37sp)

Appendix 3. 2. Number of birds captured in three different habitats: Bottom of valley (BV), Middle slope (MS) and Hilltop (HT) in Parque Estadual Intervales in southern São Paulo State. The birds were classified by guild.

Family	Specie	Guild	BV	MS	HT
Cotingidae	*Carpornis cucullatus*	C-LF		1	14
Cotingidae	*Lipaugus lanioides*	C-LF	7		
Cotingidae	*Pachyramphus validus*	E-OI	2		1
Cotingidae	*Procnias nudicollis*	C-LF			1
Cotingidae	*Tityra cayana*	C-FI			6
Emberizidae	*Cacicus chrysopterus*	U-FI			1
Emberizidae	*Euphonia pectoralis*	C-FI	2	3	5
Emberizidae	*Habia rubica*	U-FI	43	3	
Emberizidae	*Orthogonys chloricterus*	C-FI		1	1
Emberizidae	*Pipraeidea melanonota*	E-OI			1
Emberizidae	*Stephanophorus diadematus*	E-FI			2
Emberizidae	*Tachyphonus coronatus*	E-OI	6		3
Emberizidae	*Tangara cyanocephala*	C-FI			1
Emberizidae	*Tangara desmaresti*	C-FI			5
Emberizidae	*Thraupis cyanoptera*	E-OI		1	3
Emberizidae	*Thraupis ornatha*	C-FI			3
Emberizidae	*Tiaris fuliginosa*	E-OI			1
Emberizidae	*Trichothraupis melanops*	U-FI	73	26	13
Momotidae	*Baryphthengus ruficapillus*	U-FI	6	1	
Muscicapidae	*Platycichla flavipes*	C-FI	17	3	6
Muscicapidae	*Turdus albicollis*	U-FI	29	20	4
Muscicapidae	*Turdus leucomelas*	E-OI			2
Muscicapidae	*Turdus rufiventris*	E-OI	1	2	
Muscicapidae	*Turdus subalaris*	C-FI	1		
Oxyruncidae	*Oxyruncus cristatus*	C-FI			2
Parulidae	*Basileuterus culicivorus*	E-OI	4	10	4
Pipridae	*Chiroxiphia caudata*	U-FI	25	14	15
Pipridae	*Ilicura militaris*	U-FI	2	1	7
Pipridae	*Schiffornis virescens*	U-FI	10	19	14
Ramphastidae	*Baillonius bailloni*	C-LF	4		
Ramphastidae	*Ramphastos dicolorus*	C-LF			6
Ramphastidae	*Selenidera maculirostris*	C-LF	3		2
Trogonidae	*Trogon rufus*	C-FI	5	4	4
Trogonidae	*Trogon surrucura*	C-FI			2
Tyrannidae	*Atilla rufus*	E-OI		1	5
Tyrannidae	*Camptostoma obsoletum*	E-OI			1
Tyrannidae	*Elaenia mesoleuca*	E-FI	4	3	3
Tyrannidae	*Mionectes rufiventris*	U-FI	25	12	24

Family	**Specie**	**Guild**	**BV**	**MS**	**HT**
Tyrannidae	*Myarchus swainsoni*	C-FI		2	6
Tyrannidae	*Myiodynastes maculatus*	C-FI			1
Tyrannidae	*Myiornis auricularis*	E-OI	1		
Vireonidae	*Cyclarhis gujanensis*	C-FI			1
Total	***42***		270(21sp)	127(19sp)	170(35sp)

CONCLUSÕES GERAIS

LACUNAS PREENCHIDAS

As prioridades para conservação da biodiversidade geralmente levam em consideração duas perspectivas ecológicas - manutenção da diversidade de espécies e a função do ecossistemas – e uma perspectiva evolutiva - manutenção da diversidade genética dentro das populações. No entanto, estas medidas podem estar resolvendo apenas parte do problema de conservação se não forem consideradas o sistema de organização das comunidades biológicas através das interações interespecíficas e das ligações das espécies com o ecossistema (Thompson, 1997). Vários estudos demonstraram que a estabilidade e integridade de um sistema podem ser seriamente comprometidas pela redução em abundância ou perda de algumas espécies - chaves, em decorrência de suas relações interespecíficas ou pelas suas funções no sistema (Paine 1966, Terborgh 1986). Particularmente, em relação às interações interespecíficas, neste estudo foram obtidas algumas informações que poderiam ser consideradas nas medidas para a conservação:

1) Importância da estrutura vegetal e da composição de espécies de plantas para as comunidades de aves.

Este estudo mostrou que a estabilidade das comunidades de aves dependem da preservação da estrutura, complexidade e composição florística dos habitats da Floresta Atlântica. As aves exibem diferenças específicas no grau de tolerância em relação a este conjunto de variáveis bióticas. Os insetívoros e alguns frugívoros (E-OI e U-FI) são mais influenciados pelas variações na estrutura da vegetação e na forma de vida das plantas. Por outro lado, a composição de plantas é mais importante para os outros frugívoros (C-FI, E-FI e C-LF) e provavelmente para os granívoros. A dependência das espécies de aves sobre estas espécies de plantas pode estar relacionado a um processo coevolutivo. Neste caso, a extinção de uma das espécies poderia afetar as espécies à elas associadas.

Mudanças ambientais decorrentes de perturbações naturais ou antrópicas podem prejudicar determinados segmentos da comunidade de aves e beneficiar outros. As comparações realizadas entre a floresta secundária e as primárias mostraram que a perturbação antrópica em SF aumentou a densidade de plantas consumidas pelas aves no sub-bosque. Isto favoreceu a ocupação ou aumento em abundância de espécies mais móveis e generalistas como as onívoras/insetívoras de borda (E-OI) e também de espécies insetívoras (U-I e T-I) que provavelmente encontraram condições mais favoráveis de disponibilidade de insetos. Ao mesmo tempo, os frugívoros de dossel (C-FI e C-LF) foram prejudicados possivelmente pela redução de recursos neste estrato ou pela extinção de espécies vegetais importantes para estas guildas (Tabarelli *et al.* 1999).

2) Importância da heterogeneidade espacial para as comunidades de aves

A heterogeneidade espacial e complexidade estrutural verificada na Floresta Atlântica, composta por um mosaico de habitats, são elementos fundamentais no funcionamento e na estabilidade deste ecossistema. Assim é necessário que eles sejam mantidos e preservados para assegurar a viabilidade das comunidades de aves. As comunidades de aves foram caracterizadas por apresentar um equilíbrio dinâmico com flutuações temporais de composição de espécies e de abundância de indivíduos, que foram correlacionadas com as mudanças na disponibilidade de alimento. Isto sugere que muitas espécies de aves parecem se movimentar entre os habitats de acordo com as condições mais favoráveis de recurso. Foram constatadas flutuações assincrônicas na abundância mensal de frutos e nas diferenças das médias mensais das características morfológicas e nutricionais dos frutos produzidos nos habitats que devem favorecer este tipo de deslocamento pelas aves. Em nível de espécie podem ser verificadas respostas diferentes à mudança espacial e temporal na disponibilidade de frutos. Muitas espécies de aves (e.g. *Trichothraupis melanops* e *Habia rubica)* apresentam flutuações espaço-temporais em sua captura que foram correlacionadas com as flutuação na abundância de frutos. Estas espécies provavelmente expandiram sua área de vida, ou se deslocaram entre os habitats. O contrário, ocorreu com as espécies sem variações sazonais (e.g. *Carpornis cucullatus, Turdus albicollis*) que permaneceram no local e provavelmente complementaram sua dieta com uma porcentagem maior de insetos ou outras estruturas da planta de menor valor nutritivo, ou realizaram um deslocamento vertical, entre dossel e o sub-bosque. Neste caso eles foram favorecidos pela assincronia de abundância de frutos existente entre os estratos. Para as espécies de aves que apresentaram este deslocamento entre os habitats, a sua sobrevivência é garantida pela heterogeneidade espacial, que é capaz de oferecer condições mais favoráveis de disponibilidade de alimento.

A fragmentação quase sempre não amostra completamente a diversidade de habitats existente no mosaico da região, sendo que alguns tipos de habitats sempre acabam sendo perdidos. Tais fragmentos inicialmente podem conter espécies que necessitam de grandes áreas de vida, ou que apresentam um movimento sazonal entre habitats em busca de condições mais favoráveis para reprodução ou alimentação. A perda de alguns habitats pode desencadear uma alteração na densidade ou extinção destas espécies. Simultaneamente, outras espécies mais generalistas podem iniciar a ocupação destes habitats fragmentados.

3) Critérios de seleção de espécies vegetais consumidas pelos frugívoros.

No geral, as aves apresentam preferências claras e selecionam seu alimento de acordo com características morfológicas e nutricionais com alta riqueza de espécies consumidas. Alta seletividade morfológica associada à alta diversidade de espécies vegetais consumida com grandes diferenças nutricionais deve ser um requisito necessário que garante a sobrevivência das aves, porque individualmente cada espécie de fruto deve suprir a ave com uma parcela da composição nutricional requerida. Para satisfazer o balanço completo das suas necessidades corpóreas seriam necessárias várias espécies de frutos com diferenças na composição nutricional. Empobrecimento da riqueza das espécies vegetais pode afetar estas espécies de aves dependentes da riqueza de espécies pela escassez de alimento, ou pela deficiência nutricional. Estudos adicionais sobre a fisiologia digestiva das aves seriam necessários para comprovar estas idéias.

A especialização morfológica dos frutos esteve associada com o tamanho corpóreo da ave. As aves maiores tenderam a consumir frutos com sementes grandes e enquanto as aves menores selecionaram os frutos com sementes pequenas. No entanto, não pode ser obtida uma correlação significativa entre estas variáveis em função da plasticidade comportamental verificada nas aves pequenas e médias, que ultrapassam as suas limitações morfológicas impostas pela largura do bico. A riqueza de espécies de frutos presentes na dieta não esteve relacionada com o tamanho corpóreo das aves e nem com o grau de especialização das aves em relação às características morfológicas e/ou nutricionais dos frutos consumidos. As condições ambientais relacionadas à abundância e a riqueza de espécies de plantas favoreceram este tipo de dieta especializada.

LACUNAS INCOMPLETAS

Insuficiência amostral para muitas espécies endêmicas e raras - Os dados obtidos foram insuficientes para consolidar informações sobre as interações interespecíficas e os fatores bióticos relacionados com a distribuição das espécies raras e muitas espécies endêmicas, pois o número de capturas foi muito baixo. Estas informações seriam interessantes, pois poderiam justificar o padrão de distribuição e/ou raridade destas espécies na Floresta Atlântica (Goerck 1997). Um tempo maior de amostragem seria necessário, mas infelizmente, isto não tem sido possível contemplar dentro dos prazos cada vez mais curtos dos programas de pós-graduação. Além disto, é frustrante saber que o futuro destas espécies está possivelmente ameaçado em função do acelerado grau de destruição das florestas (Loiselle e Blake 1991, Turner 1996, Silva e Tabarelli 2000).

Questões marginais que estão além dos objetivos propostos – Durante o desenvolvimento das pesquisas outras questões interessantes emergiram e que poderiam ser exploradas futuramente:

- *Efeito da variação da escala espacial e temporal* – Este estudo contemplou a influência da estrutura da vegetação, composição de espécies de plantas e abundância de frutos numa escala local ao longo de um ano. É possível que haja variação na influência destes fatores, caso a distribuição das espécies de aves seja analisada em uma outra escala, por exemplo, à nível regional ou ao longo de vários anos. Neste caso, outros fatores poderiam explicar melhor o padrão de distribuição das espécies (Jordano 1993, Pearman 2002);
- *Efeito da movimentação das aves* – A movimentação das aves foi verificada apenas indiretamente por meio da flutuação mensal do número de capturas. As aves foram anilhadas, mas não houve recapturas em habitats diferentes do original. Para um estudo específico deste comportamento seriam necessários outros métodos envolvendo, por exemplo, o uso de radio-telemetria. Isto forneceria informações sobre a área de uso das espécies e poderiam ser feitas avaliações sobre o efeito deste movimento na dispersão de sementes (Westcott e Graham 2000);
- *Associação de espécies de plantas semelhantes em fenologia e na morfologia dos frutos em decorrência do padrão de deposição das sementes pelas aves* – Algumas evidências obtidas neste estudo sugerem que as aves podem influenciar no padrão de distribuição das plantas formando agregações de espécies similares tanto fenologicamente como na morfologia de seus frutos, tais como:
  (1) alta freqüência de amostras fecais com sementes de várias espécies de plantas, muitas delas, com semelhanças na morfologia dos frutos e no padrão fenológico de frutificação;
  (2) alta ocorrência de amostras fecais com sementes e/ou de sementes regurgitadas sob os indivíduos em frutificação com características morfológicas e fenológicas semelhantes às plantas visitadas.

(3) distribuição agregada de plantas de espécies diferentes com frutificação sincrônica, formando um mosaico com diferenças nos picos de frutificação entre as manchas.

Neste caso, é possível que a dispersão simultânea de diferentes espécies de plantas nas fezes das aves aumente as chances de um recrutamento e estabelecimento de indivíduos próximos com semelhanças fenológicas e morfológicas nos frutos. O aumento da incidência deste evento reforçaria o estabelecimento de indivíduos com estas características formando, consequentemente, agregações de indivíduos com frutificação sincrônica. Para a comprovação deste hipótese seriam necessários estudos sobre dispersão de sementes, padrão de deposição das sementes, recrutamento e estabelecimento de indivíduos de algumas espécies de plantas freqüentemente encontradas juntas nas fezes das aves. Além disto, seria necessário verificar o padrão de distribuição espacial destas espécies, bem como o grau de associação entre elas.

- *Contribuição para as idéias coevolutivas* - As interações coevolutivas envolvendo grupos de plantas e de aves frugívoras podem ser um reflexo das semelhanças existentes entre os componentes dos grupos em relação às características morfológicas e químicas dos frutos e digestivas e fisiológicas dos frugívoros. Isto pode ser um reflexo das afinidades taxonômicas entre as espécies, dependendo do grau de plasticidade destas características dentro dos grupos taxonômicos. Este estudo mostrou que as aves diferem quanto ao grau de especialização nos critérios de seleção dos frutos, mas esta especialização deve variar espacialmente e temporalmente dependendo da abundância e da qualidade morfológica e nutricional dos frutos disponíveis no habitat. Neste caso, parece que o efeito da pressão seletiva e a da velocidade de evolução das espécies devem ser maiores sob condições ambientais de alta abundância e riqueza de espécies. Mudanças nas condições ambientais relacionadas à alteração na abundância de indivíduos, extinção ou introdução de novas espécies no sistema podem alterar as conexões estabelecidas e modificar o rumo evolutivo das espécies. Estas idéias são parciais e incompletas, pois este estudo envolveu apenas a perspectiva do animal. Seria necessário estudar esta interação sob a perspectiva das plantas, enfocando a eficiência da qualidade de dispersão de sementes deste frugívoros especialistas. A integração destas informações poderia fornecer novas contribuições ao estudo dos mecanismos coevolutivos entre plantas e frugívoros (Howe 1993).

REFERÊNCIAS CITADAS

ALEIXO, A. 1999. Effects of selective logging on a bird community in the Brazilian Atlantic forest. *Condor* 101(3): 537-548.

GOERCK, J. M. 1997. Patterns of rarity in the birds of the Atlantic Forest of Brazil. *Conservation Biology* 11(1): 112-118.

HOWE, H. F. 1993. Specialized and generalized dispersal systems: Where does " the paradigm" stand? *Vegetatio* 107/108: 3-13.

JORDANO, P. 1993. Geographical ecology and variation of plant-seed disperser interactions: southern Spanish junipers and frugivorous thrushes. *Vegetatio* 107/108: 85-104.

LOISELLE, B. A, and BLAKE, J. G. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72(1). 180-193.

PAINE, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100: 65-75.

PEARMAN, P. B. 2002. The scale of community structure: Habitat variation and avian guilds in tropical forest understory. *Ecological Monographs* 72(1): 19-39.

SILVA, J. M. C. e TABARELLI, M. 2000. Tree species impoverishment and the future of the Atlantic forest of northeast Brazil. *Nature* 404: 72-74.

TABARELLI, M., MANTOVANI, W. and PERES, C. A. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic forest of southeastern Brazil. *Biological Conservation* 91: 119-127.

TERBORGH, J. 1986. *Keystone plant resources in the tropical forest*. Pp. 330-344. *In:* Soulé, M. E. (Ed.) Conservation biology. The science of scarcity and diversity. Sinauer Associates Sunderland.

THOMPSON, J. N. 1997. *Conserving interaction biodiversity*. Pp. 285-293. *In*: Pickett, S. T. A.; Ostfeld, R. S.; Shachak, M.; Likens, G. E. (Eds.). The ecological basis of conservation: heterogeneity, ecosystems and biodiversity. International Thomson Publishing.

TURNER, I. M. 1996. Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology* 33(2): 200-209.

WESTCOTT D. A. e GRAHAM, D. L. 2000. Patterns of movement and seed dispersal of a tropical frugivore. *Oecologia* 122: 249-257.

WITMER, M. C. and VAN SOEST, P. J. 1998. Contrasting digestive strategies of fruit-eating birds. *Functional Ecology* 12(5): 728-741.