Fruit-feeding butterfly assemblages at Dlinza and Entumeni Nature Reserves, KwaZulu-Natal: a quantitative biodiversity study

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ABSTRACT

Fruit-feeding butterfly assemblages at two indigenous forests in KwaZulu-Natal, the Dlinza and Entumeni forests were studied with baited traps during a year cycle June 2008-May 2009 and an additional March-May 2010 (autumn) survey. A total of 2801 butterflies were trapped, which consisted of 28 species, representing five subfamilies of the Nymphalidae, with the most abundant and species rich subfamily being Charaxinae. Higher than expected abundances and numbers of species trapped during the present study, though significantly lower than some tropical areas in Africa, demonstrate that this technique of quantifying assemblages with baited-traps are effective in forests of KwaZulu-Natal, South Africa and should be included in future butterfly assessments. During a mark-release-recapture survey, very few fruit-feeding butterflies were recaptured, with no observed dispersal events between the two forests. A high turnover of fruit-feeding butterfly populations reflects adequacy of habitat quality and size at both the forests for the conservation of this guild of butterfly fauna. Season had a marked effect on butterfly assemblages with optimal times of the year emerging as autumn and winter, when butterfly abundance and species richness were highest. Abundance and diversity (Shannon index) at the smaller Dlinza forest were marginally higher or at least very similar to that of the larger Entumeni forest. Higher species richness (d) was recorded at the larger Entumeni forest. A greater number of individuals and higher number of species were trapped at both forest edges in comparison to forest interior (clearings). Species richness (d) and diversity (Shannon index) at Dlinza forest were higher at the interior (forest clearings) compared to that of the Dlinza forest edge. In contrast higher species richness and diversity (Shannon index) were recorded at the Entumeni edge if compared to the Entumeni interior. Highest species richness (d) was consistently recorded at the Entumeni forest edge. Similarity between the species compositions of both forests was high.

The Entumeni forest are imbedded in a larger zone of natural grassland in contrast to the Dlinza forest which is partly located in an urban setting with small or absent grassland buffer zones. Altitudinal differences between these forests had lesser influence on the fruit-feeding butterfly assemblages whilst the closer urban edge at the Dlinza forest appears to contribute to a negative impact on the species richness at the forest margin. Recommendations to the conservation management of the Dlinza and Entumeni forests, stemming from this study, include conserving small forest remnants as part of stepping stone corridors between the forests, eradication of alien invasive plant species, conserving grassland buffer zones in which the forests are embedded and caution to any future developments in this unique area. Awareness to preserve and understand the wealth of indigenous smaller fauna, which are dependent on these magnificent forests, is to be promoted.

Key words: Fruit-feeding butterflies, quantitative techniques, habitat area, urbanization, forest edges, conservation management.

OPSOMMING

Vrugvoedende skoenlappersamestellings (gemeenskappe) by twee inheemse woude in KwaZulu-Natal, die Dlinza- en Entumeni-woude, was bestudeer met behulp van lokaasvalle gedurende ‘n jaarsiklus Junie 2008-Mei 2009 en addisionele opname Maart-Mei 2010 (herfs). ‘n Totaal van 2801 skoenlappers (=28 spesies) wat vyf Nymphalidae-subfamilies verteenwoordig, waarvan die hoogste veelheid en diversiteit onder die Charaxinae-subfamilie voorgekom het, is aangeteken. Veelheid en getal spesies was hoër as verwag en hoewel laer as wat aangeteken is vir sommige tropiese gebiede in Afrika, het die getalle gedemonstreer dat lokaasvalle in KwaZulu-Natal-woude effektief is vir kwantitatiewe opnames en in toekomstige assesseringopnames van biodiversiteit ingesluit behoort te word. Gedurende ‘n vang-merk-hervang opname is baie min skoenlappers weer gevang en geen spreidingsgevalle tussen woude is aangeteken nie. ’n Hoë omset van vrugvoedende skoenlapperpopulasies dui aan dat die kwaliteit en grootte van habitat van beide woude genoegsaam is vir die bewaring van hierdie gilde van skoenlapperfauna. Seisoen het ’n merkbare effek gehad op die skoenlappersamestellings met die herfs en winter optimale tye van die jaar wanneer die skoenlapperveelheid en spesierykheid die hoogste was. Veelheid en diversiteit (Shannon H’) by die kleiner Dlinza-woud was marginaal hoër of minstens soortgelyk aan die veelheid en diversiteit aangeteken by die groter Entumeni-woud. Hoër spesierykheid (d) is waargeneem by die groter Entumeni-woud. ‘n Hoër veelheid en groter getal spesies is gevang by woudrande in vergelyking met die binnekant van die woud (openinge in die woud). Spesierykheid (d) en diversiteit (Shannon H’) by die Dlinza-woud was hoër aan die binnekant van die woud (woudopeninge) in vergelyking met die Dlinza-woudrand. In teenstelling is ‘n hoër spesierykheid en diversiteit aangeteken by die Entumeni-woudrand in vergelyking met die binnekant van die Entumeni-woud. Hoogste spesierykheid (d) was konsekwent hoër by die Entumeni-woudrand. Spesiesamestelling tussen die twee woude was baie soortgelyk.

Die Entumeni-woud is ingebed in ‘n groter grasveldgedeelte in kontras met die Dlinza-woud wat gedeeltelik in ‘n stedelike gebied met ‘n klein of afwesige grasveldbuffersone voorkom. Verskille in hoogte bo seespieël tussen die woude blyk ‘n meer geringe invloed te hê op die vrugvoedende skoenlappersamestellings terwyl die nadere stedelike rand by die Dlinza-woud ‘n waarskynlike negatiewe impak op die spesierykheid by die woudrand het. Aanbevelings vir bewaringsbestuur van die Dlinza- en Entumeni-woude wat spruit uit die studie, sluit in die bewaring van klein woudkolle as deel van stapsteen-korridors tussen woude, die uitwissing van uitheemse indringerplantspesies, bewaring van grasveldbuffers waarbinne die woude ingebed is en sensitiwiteit teenoor enige toekomstige ontwikkelings in hierdie unieke gebied. Bewustheid van ons ryke erfenis van kleiner inheemse fauna (ongewerweldes) wat afhanklik is van die manjifieke woude, behoort bevorder te word.

Sleutelwoorde: Vrugvoedende skoenlappers, kwantitatiewe tegnieke, habitat-area, verstedeliking, woudrande, bewaringsbestuur.

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CHAPTER 1: INTRODUCTION

This study about fruit-feeding butterfly assemblages at Dlinza and Entumeni forest reserves in the Kwa-Zulu Natal Province, South Africa has been conducted for several reasons. These reasons include the testing of a quantitative technique for assessing fruit-feeding forest butterfly diversity in South African forests and descriptions of fruit-feeding butterfly assemblages in these forests. Seasonal diversity patterns, which are often lacking as a consequence of “once-off” surveys or visits by researchers, are described. Butterfly assemblage diversity is compared between the forests but also between interior forest clearings and the outer forest edges. Possible influences of broad scale ecological factors such as altitude, forest patch size and the proximity of the urban edge on butterfly assemblages in the forest are explored. This study serves as a basis for follow-up studies which could explore influences of factors such as pH of the soil, soil texture, soil structure, floristic composition and plant physiognomy on fruit-feeding butterfly assemblages. Understanding how butterfly assemblages respond to different types of matrices is essential for developing management options that ensure their survival (Muriel & Kattan 2009; Ockinger *et al.* 2009). Ultimately the study investigates the importance of conserving indigenous forests and its associated butterfly fauna in South Africa.

1.1 Importance of study

Indigenous forests in KwaZulu-Natal are under immense pressure and have been dwindling at an alarming rate, with millions of hectares having become sugarcane fields and plantations of exotic trees (Wager 1976). The total area of indigenous forest in KwaZulu-Natal is 91 201 ha which represents 1.05% of the total surface area of the province (Cooper 1985).

The present knowledge concerning fruit-feeding butterfly assemblages at these forest remnants is inadequate to address the conservation of this group of insects on the ecosystem level in South Africa. It is for example not clear to what extent there are differences in the fruit-feeding butterfly assemblages between and within forest patches in KwaZulu-Natal, and how important the conservation of all forest patches are to butterfly diversity in the region. Although the two forest patches in this study are contained in nature reserves, McGeoch

(2002) noted that baseline data is largely lacking, and the degree to which these conservation areas conserve arthropods is mostly unknown. Information available on butterfly assemblages in conservation areas are often restricted to species lists only, which originated from anecdotal information. Even seasonal butterfly data are unknown for most of the reserves and National Parks in South Africa. Therefore monitoring of butterfly assemblages, their responses to environmental changes (global warming, invasion of exotic plant species, habitat destruction) and ultimately conservation decisions are limited by the lack of quantitative comparisons of these butterfly assemblages.

Quantitative comparisons that compare assemblage structure (species richness, diversity indices) and species composition in space and time are in general rare for butterflies of South Africa and also the Afrotropical region in its entirety. A vast range of quantitative techniques including transect and point surveys, sight records and various kinds of trap-nets are available to study these insects throughout the world. Some of these methods were considered or evaluated in initial trial surveys of this study. Owing to the diversity of butterflies witnessed during preliminary surveys, and the identification skills necessary to study the diversity of butterflies of the Dlinza and Entumeni forests, it was decided to focus on fruit-feeding butterfly assemblages only. Fruit-baited traps are evaluated to determine the effectiveness of this survey technique in gathering quantitative data of fruit-feeding butterfly species in forest patches of southern Africa.

A challenge in exploring fruit-feeding butterfly assemblages in southern African forests is that quantitative techniques used for these studies have been poorly explored especially in the southern African sub-region. Another consideration is that South African forests in general contain less fruit-feeding species, such as the *Charaxes* species, compared to the lowland and montane forests from West and East Africa at the equatorial belt (Henning 1989). Therefore, this quantitative survey also explores the viability of baited traps in southern African conditions where the species richness and abundance of species may be in question.

The study included an investigation of dispersal patterns at Dlinza and Entumeni forests by means of a mark-release-recapture (MRR) technique. Understanding dispersal patterns is a fundamental step towards developing sound conservation plans (Conradt *et al.* 2001; Casula 2006), and are important in metapopulation ecology because it affects the dynamics and survival of populations (Conradt *et al.* 2001). The dispersal pattern of certain butterflies have been shown to change seasonally (Ide 2000).

Few quantitative studies that address seasonal patterns of butterfly assemblages are encountered in literature. Butterfly communities are known to be effected by seasons in many ways. For example, Summerville & Crist (2003) found species richness did not vary greatly with season, but season had a large effect on the number of individuals, and was by far the most important abiotic variable affecting community composition of forest Lepidoptera. A study by Barlow *et al.* (2007) also found there were marked differences between the total abundance of fruit-feeding butterflies in different seasons. According to Summerville & Crist (2003) phenology is an important factor affecting butterfly community composition, and should be considered in any assessment of how patch-size effects determine butterfly species diversity and distribution.

In addition to seasonal patterns, local weather can also affect butterfly communities. For instance, colonization rate was found to be zero during cold and rainy weather, contrasted with a much higher colonization rate on hot and sunny days (Néve *et al.* 1996).

On a broader scale, global warming is receiving attention in the literature and is showing to have a profound effect on butterfly communities worldwide. Recent studies show a change in the distribution and abundance of butterflies consistent with climatic warming (Hill *et al.* 2001; Braschler & Hill 2007). Phenological responses due to climate change are also expected especially at higher latitudes (Parmesan 2007), with some authors reporting an advance in the first appearance and mean flight date of species. Other responses to climate warming include a pole-ward and uphill shift in species richness and composition (Wilson *et al* 2007), which could explain the establishment of *Appias sabina phoebe* (Pierinae) in the Southern African region, whilst this species was previously only known from Mozambique and Zimbabwe (Curle & Curle 2004). If climate change is driving species distributions away from elevations where their host plant species occur, and into regions where their hosts are rare or absent, the result is a reduction in species distribution sizes, and reduced species richness (Wilson *et al.* 2007), or alternatively severe declines, or even extinctions may be the most likely outcome if climatic change occurs too fast (Stefanescu *et al.* 2003). Satyrinae, a subfamily of the Nymphalidae, shows the most notable response in comparison with other taxonomic groups (Stefanescu *et al.* 2003).

Description of the fruit-feeding butterfly assemblages at the study sites serves as a reference for monitoring possible changes in faunal composition owing to climate changes in future. The two forests studied are somewhat isolated and situated at a fairly steep altitudinal gradient not far from the coast of KwaZulu-Natal. Therefore it is likely that these forests and its associated fauna will be sensitive to marked climatic changes in future.

Numerous factors are expected to have an influence on butterfly assemblage structure and composition at forests in KwaZulu-Natal. After evaluating the success of the bait-trap technique and the quantitative description of the fruit-feeding butterfly assemblages, the possible influence of broad landscape characteristics on the butterfly assemblages will be determined. These broad landscape characteristics include altitude, forest patch area and the extent of urbanization near the forest edge.

Altitude can have a significant effect on invertebrate communities, because altitude and climate are closely correlated. These two environmental parameters are also related to many features of habitat, and can affect animal ecology in many ways (Storch *et al.* 2003). Many studies have shown marked changes in species richness in mountainous areas. For example, an unexpected increase in butterfly species richness with increasing altitude was found by Wettstein & Schmid (1999), which was attributed to the higher habitat diversity adjacent to the high altitude sites. However the abundances of several arthropods were found to decrease with increasing altitude (Wettstein & Schmid 1999). Species richness was also found positively correlated with elevation in the Toquima range, and to increase with altitude (Mac Nally *et al.* 2003). A partial explanation for this could be that habitats with a range of elevations will have higher habitat heterogeneity and therefore different within-habitat microclimates (White & Kerr 2007). A study by Pyrcz & Wojtusiak (2002) found a middle elevation peak in species richness due to an overlap of lower and higher elevation species distributions. However, according to Begon *et al.* (1996), species richness generally shows a decline with increasing altitude, due to isolation and smaller habitats at higher elevation.

Owing to habitat loss forests in KwaZulu-Natal are relatively small isolated patches. This habitat fragmentation can affect butterfly communities in many ways. Specialist species are known to be affected by patch area more than generalist species (Natuhara *et al.* 1999; Krauss *et al.* 2003; Kitahara & Fujii 2005). Therefore generalist species may have higher abundances in disturbed areas (Ockinger *et al.* 2009; Bergerot *et al.* 2010). There are also reports of a decline in abundance of widespread species especially in vegetation types outside nature reserves such as farmland and urban areas (Van Dyck *et al.* 2009). Another consideration is that large bodied species are more affected by habitat area than smaller butterfly species (Benedick *et al.* 2006).

Patch area is also known to have an effect on butterfly population densities, however these effects are known to be diverse, and has shown to be controversial in literature. While some studies have found butterfly population densities to be significantly positively related to habitat area for both generalist and specialist butterfly species (Krauss *et al.* 2003), others report an unexpected decrease in population densities of oligophagous and polyphagous species with increasing habitat area (Steffan-Dewenter & Tscharntke 2000). Fruit-feeding butterfly species have also shown to vary in their response to habitat area. During a study in the Brazilian Atlantic forest, Uehara-Prado *et al.* (2007) found certain species which were abundant in small forest fragments but absent in the larger reserve, and other species which were common in the larger reserve and had low abundance in the small fragments. These responses to habitat area are however not limited to Lepidopteran species, as other insects also showed similar trends to patch area. According to Donaldson *et al.* (2002) the abundance of particular pollinator species varied in their response to habitat patch size with bees and monkey beetles significantly affected by fragment size.

Species richness in a fragmented environment is expected to follow the theory of island biogeography, and should be higher in larger habitats, and decrease with increasing isolation (Vandewoestijne & Baguette 2004). Many studies support this theory. For example, butterfly species richness in rain forest remnants in Borneo were significantly positively correlated to remnant size (Benedick *et al.* 2006), and several other studies also reported a greater number of butterfly species with increasing patch area (Wettstein & Schmid 1999; Lehmann & Kioko 2000).

However in contrast to the above findings several authors have found different trends. A study in South Africa by Donaldson *et al.* (2002) found that the overall species richness of bees, flies, and butterflies did not vary significantly among different sized fragments. The latter findings were in Renosterveld (Fynbos biome) which are different from forest environments. Cottrell (1985) found that a number of Fynbos butterfly species are less dependant on

Capensis Flora elements. In proper forest environment Larsen *et al.* (2009) found that the tiny forest patch Wli Falls (3km^2) in Ghana had far more butterfly species than the much larger Kyabobo (218 km^2) forest fragment. According to Uehara-Prado *et al.* (2007), patch size was reported to have no significant effect on the species richness of fruit-feeding butterfly species during a study in the Brazilian Atlantic forest. However, it is generally accepted that lower species richness are present in very disturbed habitats (Kocher & Williams 2000; Henning *et al.* 2009).

As with abundance and species richness, butterfly diversity in a fragmented environment has also shown to be positively correlated to patch area (Benedick *et al.* 2006), while other studies showed no significant differences in the Shannon diversity indices between patch size and even small areas of < 1 ha contained a high diversity of insects (Donaldson *et al.* 2002). According to Natuhara *et al.* (1999) diversity is lower in a fragmented landscape.

The higher diversity at larger patches is mainly a consequence of the greater variation in topography, which provides different climatic, edaphic, and vegetative conditions (Kocher & Williams 2000), while the higher species richness in a fragmented environment can be due to mosaic effect (Natuhara *et al.* 1999). WallisdeVries (2003) states that preservation of small forest fragments is extremely important, especially for endangered butterfly species with limited dispersal ability.

Less mobile species cannot readily disperse between patches (Natuhara *et al.* 1999), with limited dispersal in smaller populations being associated with increased extinction risk (Schultz & Cronje 2004), due to lower genetic diversity (Vandewoestijne & Baguette 2004). Evidence is accumulating that extinction may be a regular feature of the dynamics of many butterfly populations (Erhlich 1989; Boggs *et al.* 2000). Therefore maintaining of viable population networks (metapopulations) is crucial to butterfly survival (Brereton 2004). However dispersal between patches may be limited by low connectivity, as the majority of Afro-tropical butterflies depend on forests for their survival and are reluctant to cross inhospitable terrain (Larsen 1991). For some species, even narrow bands of unsuitable habitat act as effective barriers to movement (Natuhara *et al.* 1999).

In addition to smaller patch sizes and limited dispersal in fragmented environments, these landscapes generally have more habitat edge exposed (White & Kerr 2007; Vu 2008). Many studies have indicated marked differences in butterfly forest edge communities. For example, during a study in Vietnam, Vu (2008) found species richness and abundance of butterfly communities were low in the natural closed forest, and highest in forest edges, however forest edge recorded a lower diversity index when compared to the forest interior. In Japan differences were also found between forest interior and forest edge, where butterfly species diversity and species richness was found to be higher at forest edges when compared to forest interior sites, which was attributed to a higher plant species richness and diversity at these forest edges, resulting in greater abundances of univoltine, specialist, and low population density species (Kitahara & Watanabe 2003). During a study in Kenya at two forest patches, Rogo & Odulaja (2001) also found a similar trend of higher diversity and species richness at the forest edge of Mrima forest . In contrast Rogo and Odulja (2001) found a lower butterfly species richness and diversity than the forest interior, at a smaller degraded Muhaka forest. This Muhaka forest had high anthropogenic disturbance, resulting in an open canopy and a large network of footpaths, creating many edge effects within the forest interior. According to Ries & Debinski (2001), edge responses are highly variable and depend on the species, edge characteristics, and the local environment.

A study on edge effects by Ries & Sisk (2008) found butterflies respond either negatively or positively to habitat edges, with a positive response resulting in an increase in butterfly densities at the habitat edge, and a negative response a decrease in population density at the habitat edge in comparison to habitat interior. Butterflies avoid edges adjoining non-habitat or low quality habitats that offer only supplementary resources, and they show increased densities near edges which have high quality habitat or habitat that contains complementary or different resources. According to Ries & Sisk (2008) the separation of resources must be very stark in order to trigger positive edge responses.

Urban reserves usually have a marked change in vegetation structure between the edge and the surrounding landscape, which provides an excellent opportunity to study the effects of habitat fragmentation on invertebrate communities (Ockinger *et al.* 2009). Forests in this study have a natural marked edge because they are embedded in grasslands. An urban edge effect on the Dlinza forest, which is located at the boundaries of the town of Eshowe, remains a possibility and is considered in this study.

It is important to note that studies on the distribution of butterfly species in landscapes with different degrees of disturbance have shown controversial data in literature (Uehara-Prado *et al.* 2007). For example, a study by Ockinger *et al.* (2009) found no effect of the urban area on butterfly species richness or density. A study conducted in Colorado also showed the extent of the surrounding urban landscape had no significant effect on species richness and composition of grassland butterflies (Collinge *et al.* 2002).

Studies relating to the effect of urbanization on fruit-feeding butterfly assemblages are lacking in literature, however this butterfly group is reported to be adapted to naturally heterogeneous or disturbed environments (Lewis 2000; Uehara-Prado *et al.* 2007). While natural disturbance may or may not mimic human-produced disturbance (Kocher & Williams 2000) this apparent resilience to naturally disturbed environments may provide these butterflies with an ability to be less affected by anthropogenic disturbance than other butterfly groups. However these butterflies are not immune to fragmentation and are known to undergo a change in species composition with habitat disturbance (Uehara-Prado *et al.* 2007), which makes them valuable as indicators of land-use change (Barlow *et al.* 2007).

Effects of habitat change on the fruit feeding butterfly assemblages may also depend on spatial scale. According to Ribeiro *et al.* (2008), fruit-feeding butterfly assemblages are known to be affected by landscape diversity on varying spatial scales. Other studies found butterfly assemblages in a patch are affected by the surrounding landscape on quite large spatial scales (Bergman *et al.* 2004), while another study found landscape context was more important at small spatial scales in that landscape diversity within a radius of 250 m best predicted species richness (Krauss *et al.* 2003).

Another consideration with reference to invertebrates in an urban area is the effect of pollution. During a study in India, Jana *et al.* (2006) found the insect orders Lepidoptera, Hemiptera, and Orthoptera were affected by pollution from industrial areas, which makes these groups valuable as bio-indicators for identifying degrading communities.

Often contrasting findings on butterfly assemblages in spatial and temporal scales or the overall lack of knowledge outlined in the previous paragraphs show how much research remain on this challenging topic of studying butterflies on the assemblage level in ecology.

According to McGeoch (1993) an understanding of anthropogenic induced effects on invertebrate communities is essential if an attempt is to be made to reduce the impact of human activity and conserve biodiversity, and this should be the primary goal of all conservation efforts.

1.2 Research aims and objectives

The main research aims and objectives are guided by the importance of the study in the previous section. This biodiversity study focuses on properties which emerge from the results, therefore a number of hypotheses are given. A main research aim of the study is to acquire knowledge that will enhance the conservation of butterfly assemblages and future research about butterfly assemblages in African forest patches. Biodiversity studies are by nature multifaceted and as a consequence a number of research questions and objectives could be addressed by interpreting patterns that emerge from such studies. Research questions and objectives that are stated in the initial paragraph of this section are addressed in the predictions and hypotheses that follow:

The following predictions were made:

1) Hypothesis 1: Fruit-baited traps are useful to study the fruit-feeding butterfly assemblages in South Africa but are limited by a relatively low number of species and abundances in a sub-tropical environment (if compared to tropical environments)

2) Hypothesis 2: Mark-release-recapture technique will show a moderate turnover of species which may imply moderate abundances of species, with a lesser turnover at the smaller Dlinza forest.

3) Hypothesis 3: Seasons are expected to influence species abundance and species richness. An optimal time for fruit-bait surveys will be in late summer or autumn.

4) Hypothesis 4: Forest edge assemblages at both reserves have higher species richness and diversity on average compared to species richness and diversity from forest interior survey points.

5) Hypothesis 5: Altitudinal differences between the two forests are relatively small in the context of the regional landscape and will show limited differences such as reflected by more coastal versus more inland species.

6) Hypothesis 6: Entumeni being the larger of the two forests and situated in a rural setting, will have a higher species richness and species diversity in comparison to Dlinza forest which is smaller and situated in an urban environment with higher anthropogenic influences at its edges.

CHAPTER 2: STUDY AREA

2.1 Location

The study was carried out at two indigenous scarp forest reserves in KwaZulu-Natal, South Africa, near the town of Eshowe approximately 136 km north east of the city of Durban (Fig. 1). The two forests, Dlinza and Entumeni, are located between 28^{o} and 29^{o} south latitude and between the Tugela and White Umfolozi rivers. The study area is located 28 to 35 km from the coast and at altitudes of 540 to 700 m above sea level.

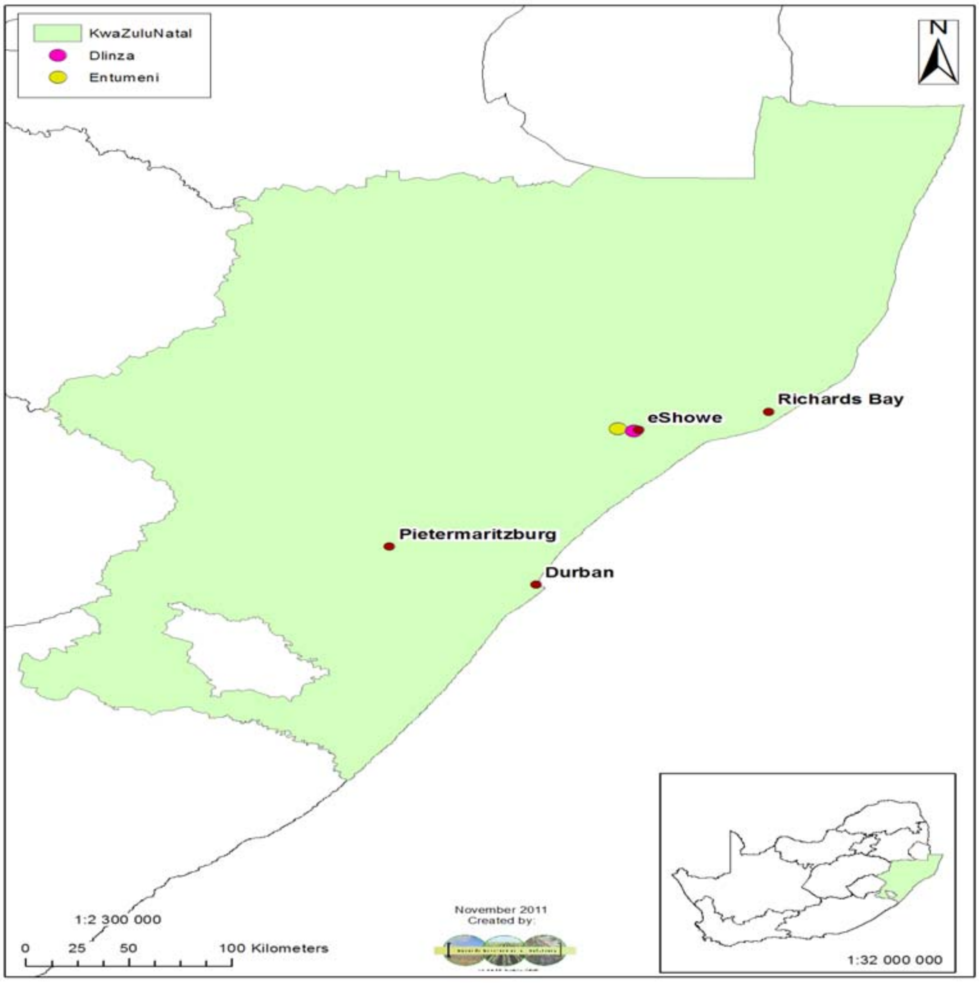


Fig. 1. Map of KwaZulu-Natal Province showing the town of Eshowe, and the location of Dlinza and Entumeni Nature reserves.

2.2 Geology and soil

Both these forest patches occur on sandy soils on slopes of varying inclination (5–40°). The soil is very sandy (average 83% sand and 9% clay), acidic (average pH of 3.8) and has a resistance of 714 ohms. The nutrient status of soils are moderate (3.5 cmol/kg Ca, 42.1 mg/kg P, 1.5 cmol/kg Mg, 33.3 mg/kg Na, 206 mg/kg K and 7.3% C). Dead leaf litter cover is high (average: 91 %) (Mucina *et al.* 2007). In general scarp forests soils are nutrient poor and leached (Mucina & Rutherford 2006) which underlines the importance of dead leaf litter for the maintenance of these forests.

2.3 Climate

Mean annual rainfall varies from 947–1155 mm (average: 1 045 mm). Fog probably contributes to total precipitation, but apart from number of fog days per year (53 days) the amount is unknown. Temperatures range from 12ºC (minimum) to 24ºC (maximum), with a mean of 18–19ºC (Mucina *et al.* 2007). Coastal influence moderates minimum temperature in the coastal region (Mucina & Rutherford 2006). Though the Dlinza and Entumeni forests are a distance of 28 to 35 km from the coast these two forests are possibly close enough for the coast to have a stabilizing effect in terms of temperature and moisture.

2.4 Vegetation

Dlinza and Entumeni forests are part of the Forest biome which covers just more than 0.1% of the land surface of South Africa (Mucina & Rutherford 2006). Forest stand dynamics are determined by a number of important processes inside the forests, such as natural disturbance and gap dynamics, litter fall and a closed nutrient cycling, characteristic fruit and seed types and associated regeneration processes, and plant-animal interactions (Mucina & Rutherford 2006).

Both the forests are part of the Scarp Forest vegetation type (Mucina & Rutherford 2006). These forests are described as tall, species rich and structurally diverse, with well-developed canopy and understorey tree layers, but a poorly developed herb layer (Mucina & Rutherford

2006). Patches of this Scarp Forest are located as far as 140 km inland (Mpumalanga), but extend increasingly closer to the sea in a southward direction – in Pondoland, and southern Transkei they occur at the coast or in deep gorges, often associated with krantzes, scarps and coastal platforms (Mucina & Rutherford 2006). Most of the patches occur at low altitudes between 50 and 600 m. Biogeographically and from a biodiversity point of view this is probably the most valuable forest type in South Africa, housing many endemic species, six endemic genera and one endemic family (Rhynchocalycaceae) of trees and relict occurrences of small populations of *Encephalartos,* suggesting that this vegetation unit is biogeographically ancient (Mucina & Rutherford 2006).

Mucina *et al.* (2007) identified plant communities at Dlinza and Entumeni forest reserves as *Philenoptera sutherlandii–Clivia miniata* Community. These communities are closed-canopy forests and are up to 35 m tall, occurring on sandy soil of the Arcadia type—all situated in or near Eshowe, KwaZulu-Natal. The tree layer comprises *Albizia adianthifolia, Drypetes gerrardii, Philenoptera sutherlandii, Trichilia dregeana, Croton sylvaticus* and *Cussonia sphaerocephala.* The upper and lower shrub layers are dominated by, among others, *Carissa bispinosa* subsp. *zambesiensis, Dalbergia armata, Dracaena aletriformis, Duvernoia adhatodoides, Englerophytum natalense, Mackaya bella, Rinorea angustifolia, Rothmannia globosa* and *Tricalysia capensis*, while the herb layer is well developed and dominated by, among others, *Cyperus albostriatus, Dietes iridioides, Oplismenus hirtellus* and *Prosphytochloa prehensilis*. Epiphytes are rare (Mucina *et al.* 2007).

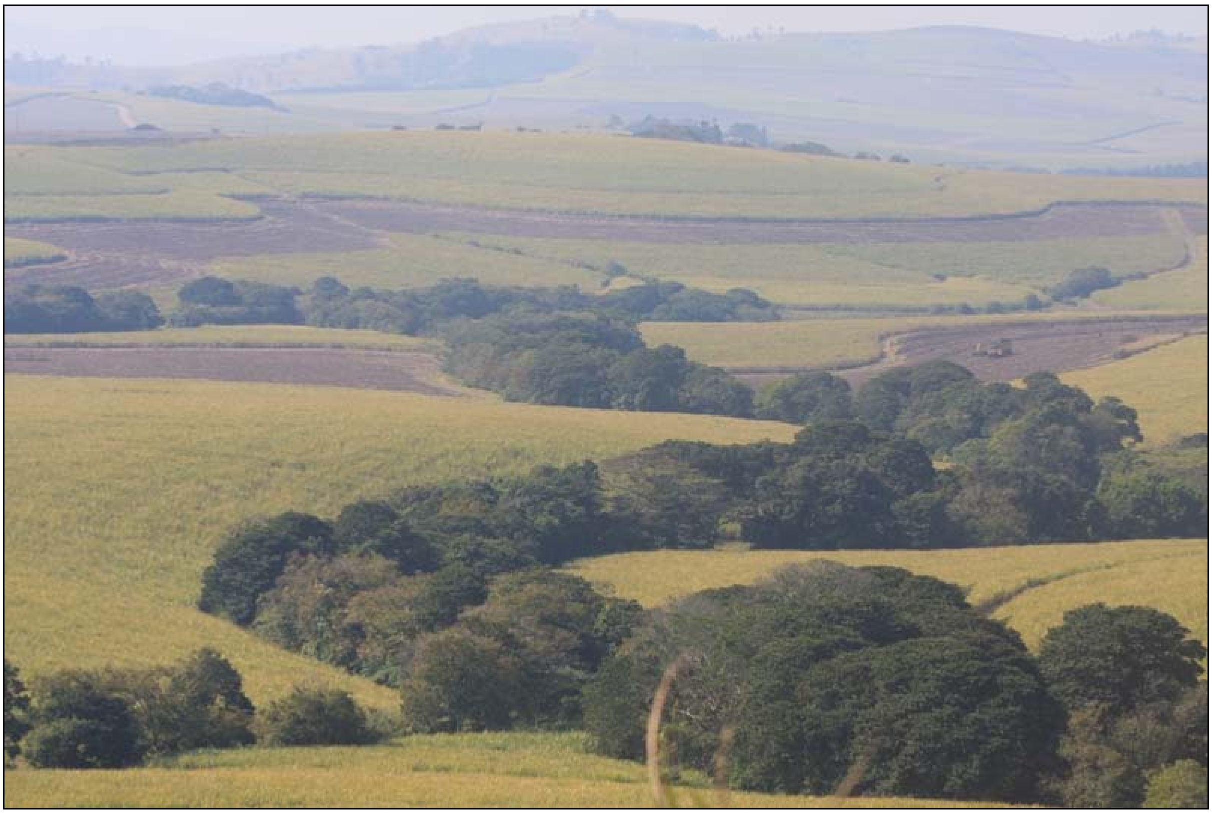


Fig. 2. View of landscape between Entumeni and Dlinza forests showing the linear forest pockets and sugarcane monocultures.

2.4.1 Diagnostic Species:

Asplenium aethiopicum, A. theciferum var. *concinnum, Chlorophytum bowkeri, Clivia miniata, Cussonia sphaerocephala, Cyperus albostriatus, Dumasia villosa, Elaphoglossum acrostichoides, Mackaya bella, Oxyanthus speciosus* subsp. *gerrardii, Philenoptera sutherlandii, Prionostemma delagoensis, Prosphytochloa prehensilis, Siphonoglossa nkandlaensis, Strychnos decussata, Tabernaemontana elegans, Tricalysia capensis, Urera trinervis.*

2.4.2 Constant Species

Asplenium rutifolium, Carissa bispinosa subsp. *zambesiensis, Clivia miniata, Cussonia sphaerocephala, Cyperus albostriatus, Dietes iridioides, Drypetes gerrardii, Englerophytum natalense, Mackaya bella, Monanthotaxis caffra, Oplismenus hirtellus,* *Oxyanthus speciosus* subsp. *gerrardii, Philenoptera sutherlandii, Prosphytochloa prehensilis, Rawsonia lucida, Rinorea angustifolia, Trichilia dregeana, Asparagus virgatus, Asplenium aethiopicum, Behnia reticulata, Bersama tysoniana, Cassipourea gummiflua* var. *verticillata, C. malosana, Chlorophytum bowkeri, Cnestis polyphylla, Dioscorea cotinifolia, Dracaena aletriformis, Dumasia villosa, Flagellaria guineensis, Peddiea africana, Strychnos decussata, Teclea natalensis, Tricalysia capensis* (Mucina *et al.* 2007).

2.4.3 Locally dominant species

Drypetes gerrardii, Philenoptera sutherlandii

2.4.4 Vertical and horizontal structure

All vegetation layers are well developed and distinct. Canopy emergents reach up to 35 m (average: 27 m), with cover estimates ranging from 20–100% (average: 71%). The canopy layer is 11–22 m high, with cover estimates ranging from 25–98% (average: 60%), while the subcanopy layer is 3–12 m high, with cover estimates ranging from 6–35% (average: 23%). The upper shrub layer has cover estimates of 9–25% (average: 16%). Cover values for the lower shrub layer are 5–33% (average: 14%). The cover of the herb layer varies considerably (range: 4–60%; average: 17% (Mucina *et al.* 2007).

2.5 Site descriptions

2.5.1 Dlinza

This forest was established as a nature reserve in 1947. It is the smaller (250 ha) of the two forests and is situated 28 km from the coast at 540 m.a.s.l in the urban environment of the town of Eshowe. The forest is popular with tourists and receives many visitors throughout the year the majority of which come to view the rich birdlife. Although anthropogenic disturbance is minimal at the interior of the forest, the surrounding area has various forms of land-use types such as urban development, sporting facilities, and agricultural lands. The forest is also surrounded by paved roadways (Fig. 3).

A unique feature of the forest is a 125 m aerial boardwalk which extends 10 m above the forest floor and ends with a 20 m high steel viewing tower which allows visitors to experience canopy life (Fig. 4). Although world renowned for its birdlife, more than 80 species of butterflies have been recorded from Dlinza forest, with Emperor swallowtail (*Papilio ophidicephalus)*, Gaudy commodore *(Junonia octavia sesamus),* Mocker swallowtail (*Papilio dardanus cenea),* White-banded swallowtail (*Papilio echerioides echerioides*), Mother of pearl (*Protogoniomorpha parhassus*) being just a few of the species present (O' Reagain 2001). Eight *Charaxes* species have been recorded from the forest and several butterfly enthusiasts have in the past collected and drawn up species lists of this subfamily.

Fig. 3. Dlinza forest edge and location of the first forest edge sample site DE1.

Fig. 4. Metal viewing tower in Dlinza forest reserve. Location of the first forest interior sample site.

2.5.2 Entumeni

The Entumeni forest was declared as a nature reserve in 1970. It is not as well known as Dlinza forest, and receives fewer visitors, although it is situated on the KwaZulu-Natal birding route. It is the larger of the two forests (750 ha) and is situated in a rural environment around 7 km directly west of Dlinza at an altitude of approximately 700 m. The surrounding landscape consists of sugarcane monocultures, exotic tree plantations and small indigenous forest patches. The topography at Entumeni is significantly steeper than Dlinza forest and is surrounded by a number of large grassland areas. The forest is located within a large gorge at the base of which flows a river.

The grassland where the edge survey sites are located measures approximately 420 m from north to south and 430 m from east to west, and has large expanses of ferns and forbs. The area is grazed by herds of zebra and is occasionally subjected to controlled burning (Fig. 5). The area slopes from east to west with the forest edge at a lower elevation than the surrounding grasslands. The forest edges are significantly steeper and more undulating in comparison to Dlinza forest edges which are mainly on level ground (Fig. 6).

Fig. 5. Entumeni forest edge showing the grasslands and undulating topography.

Fig. 6. Entumeni forest showing the rural environment with surrounding grasslands.

CHAPTER 3: MATERIALS AND METHODS

3.1 Sampling procedure

Butterflies were trapped at the two forests, Dlinza and Entumeni, using baited traps over two survey periods. The first survey was conducted over a twelve month period from June 2008 to May 2009 and a second Autumn survey during 2010 consisting of three months from March to May 2010. The second survey was conducted to verify the high abundance and species richness observed during Autumn 2009. During the first twelve month period surveys were conducted in all four seasons that included the rainy and dry season.

During preliminary surveys at the two forests, which explored the use of different techniques, it was realized that there was a relatively high diversity of butterflies at Dlinza and Entumeni forests. For this reason, efforts were focused on the fruit-feeding butterfly guild and using the baited trap technique (Figs 8, 9). This eliminated the problem of species identification posed for butterflies belonging to the families Hesperiidae and Lycaenidae which can be very difficult to identify. Fruit-feeding butterfly species are abundant in these forests and the species richness of this group of insects are known to be positively correlated with other butterfly groups which make them good indicators of the status of the entire butterfly community in a region (Horner-Devine *et al.* 2003).

The number of days of sampling per month at each forest differed owing to weather constraints. Weather during some days was far less favourable for adult butterflies to be active ("bad days"). To compare assemblage structure the four days with the highest abundance were chosen from each season (winter, spring, summer, autumn) for both forests. This culminated in 80 trap hours at each forest for the first study and 15 trap hours for each forest for the Autumn 2010 study.

Baited traps were hung in sequence, starting with the first forest interior survey point, and ending with the third forest edge survey point. These points were sampled in the same order to ensure a uniform capture time for each sampling site. Traps were suspended by wire hooks from tree branches near to the ground. The only exception was the first interior survey point at Dlinza forest which was located on the aerial boardwalk 20 m above the forest floor. Baited traps were hung before or as close to 09.00 and were sampled at 14.00 with no repetitions. As far as possible traps were positioned to ensure the maximum amount of direct sunlight, as sunlight appears to attract more species to the traps. This strategy was followed due to personal observation during trial surveys.

At each sampling occasion quantitative data was collected whereby every butterfly was identified, recorded, and then released at the point of capture. For the Mark-Release-Recapture (MRR) study all individuals were marked with nail polish on the underside of the left rear wing with a unique mark to identify the particular sampling site and each forest was assigned a separate colour. If the identification of a butterfly was ever in doubt, a voucher specimen was taken to be identified later with field guides. However, collecting of specimens were kept to a minimum to reduce the effect of removing individuals over time. After sampling, traps were removed and re-deployed at each sampling occasion. As far as possible cold and wet weather was avoided as fruit-feeding butterflies are inactive during cold weather.

3.2 Identification of species in the field

Butterflies pose a challenge for accurate identification, especially for the novice in the field. Identification problems can be exacerbated by sexual dimorphism and mimicry, as well as the different seasonal forms which occur for certain butterfly species. According to Henning (1989) there is a strong presence of sexual dimorphism in some species of Charaxinae.

During the trial runs, much time was devoted to on site training of identification by an experienced Lepidopterist (R.F. Terblanche, more than forty years of field experience). The researcher also spent many hours of self study in the field with the aid of field guides as well as specialized works. Field guides included Woodhall (2005), Migdoll (1987) and Williams (1994) and more specialized works included Pringle *et al.* (1994) and Henning (1989). Identification and the time to obtain identification skills can be time consuming. However, once a good skill has been developed, a significant amount of data can be collected in a relatively short space of time.

3.3 Design

There were six sampling sites at each forest patch, three at the forest interior, and three at the forest edge (Fig. 7). The forest interior sites were randomly selected where tree fall gaps were present, were large enough to allow sufficient sunlight to enter the glade, and butterflies to circle and enter the trap without interference from the canopy of trees. The only difference at Dlinza forest was that the first forest interior sampling site was located on the aerial boardwalk viewing tower which is 20m above the forest floor. Forest edge sampling sites were positioned around the perimeter of the forest. Due to the relatively large size and steep topography at Entumeni forest, the three forest edge sampling sites were all located on the north eastern side of the forest near to the forest entrance and access road. Each trap was ≥200 m apart to ensure that unbiased and independent sampling occurred and was a true representation of the butterfly assemblage in that area of the forest.

Sampling sites were named Dlinza interior one, two, and three and Dlinza edge one, two, and three and were abbreviated as DI1, DI2, DI3, and DE1, DE2, and DE3 (Table 1). An identical design was adopted at the larger rural Entumeni nature reserve, where sampling sites were named Entumeni interior one, two and three, and Entumeni edge one, two, and three and abbreviated as EI1, EI2, and EI3, and EE1, EE2, and EE3. For the remainder of this thesis the abbreviation will be used when referring to a certain sampling site.

Fig. 7. Aerial photograph of Entumeni and Dlinza forest nature reserves showing sampling sites, and extent of urbanization surrounding the smaller Dlinza nature reserve.

3.4 Sampling sites

Table 1. Summary of the twelve sampling sites indicating altitude, grid references, and a brief description of the site.

Sampling site	Altitude	Grid reference	Description
DI1	531 m	28°53ʹ36. 4″S 31°27ʹ09.1″E	Located in the canopy on the viewing tower approximately 20 m above the forest floor. Due to the unique position of this survey point, visitors to the forest regularly pass this bait trap in order to gain access to the upper-level of the viewing tower.
DI2	508 m	28°53ʹ42.9″S 31°27ʹ02.1″E	Located on a forest pathway in a large forest clearing. This site has a greater structural complexity in the vegetation, and has a small stream running through the site.
DI3	531 m	28°53ʹ47.7″S 31°27ʹ14.7″E	Was located adjacent to a forest gravel roadway which does occasionally receive vehicle traffic.
DE1	534 m	28°53ʹ28.2″S 31°26ʹ52.7″E	This sample site was positioned on the northern side of the forest in a cemetery. The area has mown grass and a 3 m high *Duranta* hedge separating it from a main paved roadway. This sampling site is in close proximity (30 m) to residential housing
DE2	543 m	28°53ʹ32.2″S 31°27ʹ02.0″E	Was also located on the northern edge of the forest in close proximity to the forest main entrance and parking area. The area consists of both a well mown grass area which is allocated for recreational purposes, and an expanse of

			ferns and grasses which are on occasions subjected to controlled burning. This site was located further from a paved road and houses than DE1.
DE3	501 m	28°53ʹ43.6″S 31°27ʹ36.5″E	Was located on the south-eastern side of the reserve adjacent to Royal Arch drive in a crescent shaped grassland area approximately thirty meters from a tarred road.
EI1	642 m	28°53ʹ10.3"S 31°22ʹ33.9"E	Located on a forest pathway adjacent to a large open glade.
EI2	649 m	28°53ʹ18.8"S 31°22ʹ42.4"E	Also on a forest footpath in a similar environment to the other two forest interior survey points.
EI3	612 m	28°53ʹ25.4”S 31°22ʹ40.2"E	This sampling site was also positioned on a forest pathway, however at a lower elevation than the other two forest interior trap stations.
EE1	675 m	28°52ʹ59.9”S 31°22ʹ48.6"E	Was the closest sampling site to the forest entrance gateway, and was located near a small stream.
EE2	660 m	28°52ʹ52.6"S 31°22ʹ46.7"E	This sampling site was located the furthest from the gravel access road, and was sheltered from wind by the surrounding landscape.
EE3	701 m	28°52ʹ50.9"S 31°22ʹ59.0"E	This site was the furthest point from the entrance to the forest and was located approximately 50 m from the gravel road which leads to the forest entrance and adjacent farmlands.

Only broad scale ecological characteristics were noted at each sampling site such as: altitude, forest patch size and the proximity of the urban edge. Detailed measurements of environmental parameters such as pH of the soil, soil texture and structure fell beyond the scope of this study. However information available from previous plant studies such as mentioned in Chapter 2, Study Area, is used as reference.

3.5 Data collection

Fig. 8. Baited trap at Entumeni forest edge showing circular board and zipped opening at the top of trap for retrieval of butterflies

Fig. 9. Base of baited trap showing entry point for butterflies and *Charaxes candiope candiope* feeding.

Adult butterflies are divided into two main groups based on their feeding behavior, either nectar feeding or fruit-feeding. The fruit-feeding guild belongs exclusively to the family Nymphalidae, and feed on fermented fruit and plant sap.

Many of these butterfly species such as the *Charaxes* species are very swift fliers and therefore not easily collected except by trapping (Henning 1989). For this reason the use of fruit-baited traps are necessary for studying this butterfly group. Some authors suggest that traps are a necessary component of butterfly surveys (Larsen *et al.* 2009), and without the use of baited traps more than half the Charaxinae and some of the *Bicyclus* will be missed (Larsen 1991).

There are other advantages with using this survey technique such as being able to sample many areas in a forest patch simultaneously, as well as eliminating the problem of species identification experienced with other popular survey techniques such as transect and point surveys (Lewis 2000).

In this study the trap design was a simple cylindrical tube made from a mesh material which measured approximately 1.02 m high x 0.24 m in diameter (Figs 8, 9). Each trap was sealed at the top and open at the bottom with a round wooden board suspended below the trap on which attractant was placed. A zipped opening at the apex of the net made it easier to remove butterflies when emptying the bait traps.

Due to the simple design butterflies did occasionally escape from the traps. However once they entered the trap they usually gathered near the top of the trap and seldom moved down and escaped unless the bait trap was moved or disturbed.

The main ingredient of the attractant was fermented banana and pineapple. To this mixture sugar, and yeast was added (to accelerate fermentation) and left to ferment for three days. Each time new attractant was made the mixture was standardised as far as possible by using the same amount of bananas, pineapple to which 2 tablespoons of sugar and a small packet of brewer’s yeast was added. After two days of trapping a new mixture was made to ensure that the mixture was as uniform as possible for all sampling occasions.

3.6 Statistical analysis

Of the overall 2801 butterflies trapped, only 2438 observations were used for the statistical analysis. This was done in order to standardize the data for comparative purposes by eliminating days on which the weather was too bad. A protocol developed by Terblanche & Edge (2011) that includes an assessment of the optimality of weather conditions (temperature, clarity of sky, stillness of wind, lack of precipitation) was used. Data for 8 days of sampling were selected from each season for the first study period, and 4 days for each forest representing days which had the highest butterfly abundance.

For the second survey period (in autumn 2010) a total of 6 trap days were used for the data analysis, 3 from each forest with no data omitted from the analysis.

To express community variation a data table was compiled for each study period, whereby the number of individuals and the number of butterfly species were pooled for each of the 12 sampling sites. Indices of richness, evenness, and diversity of butterfly communities were assessed for each habitat type and were calculated using Primer V5 software (Primer –E Ltd, 2001).

Diversity indices of each sampling site were calculated using the following formula:

$$H = \sum_{i=1}^{s} Pi \ln Pi$$

Where s=total number of species and $p_{i=}$ the relative abundance of the *i*th species.

Species richness (d) (Margalef's) indices of each sampling site were calculated using the formula:

$$d=(S-1)/\mathrm{Log}\ (N)$$

Statistica (STATSOFT Version 9) was used to compare the overall means in abundance, species richness (d), and Shannon diversity (H) between forests, and the means between forest interior and edge at each forest patch and between landscapes.

T-tests were also calculated with Statistica (STATSOFT Version 9) by way of independent samples to determine whether there were any significant differences in the mean abundance, species richness (d), and Shannon diversity (H) indices. Variation in species composition between sites was investigated using Detrended Correspondence Analysis (DCA).

CHAPTER 4: RESULTS

4.1 Broad summary

4.1.1 Mark-release-recapture study

In total 2801 butterflies were recorded with baited traps at Dlinza and Entumeni forests over both study periods, June 2008-May 2009 and March 2010-May 2010. The Mark-Release-Recapture (MRR) study, during which 2074 butterflies were marked and released at the two forests, was only conducted for the period June 2008-May 2008. Only 11 recaptures were recorded for both forest patches, with 9 recaptures recorded at Dlinza forest and 2 recaptures at the larger Entumeni forest (Table 2). There was no dispersal recorded between forest patches, however there were some interesting dispersal events within each forest remnant especially at the smaller urban Dlinza forest reserve (Table 2).

Most recaptures were stay at home events and these butterflies were recaptured in the same location where they were marked. However there were several dispersal events from the forest interior to the forest edge, with a couple of movements around the forest fringe from one forest edge survey point to another (Table 2). Most butterflies recaptured were from the subfamily Charaxinae, while only one recapture was from the subfamily Biblidinae (Table 2).

Table 2. Dispersal events of fruit-feeding butterflies recorded with baited traps at Dlinza and Entumeni forests during first study period June 2008-May 2009.

SPECIES	**Recapture 1**	**Recapture 2**	**Recapture 3**
Charaxes brutus natalensis	Marked at DI1and recaptured at DE2		
Charaxes cithaeron	Marked at DI3 and recaptured at DI3	Marked at DI1and recaptured at DE1	
Charaxes ethalion	Marked at DI2 and recaptured at DE2		
Charaxes varanes	Marked at DI2 and recaptured at DE1	Marked at DE2 and recaptured at DE1	Marked at DE2 and recaptured at DE2
Charaxes xiphares	Marked at DE2 and recaptured at DE2	Marked at DE2 and recaptured at DE2	Marked at EI2 and recaptured at EI2
Eurytela hiarbas	Marked at EE1 recaptured at EE2		

4.1.2 Outline of total of butterfly species, subfamilies and abundances

Owing to inclement weather and corresponding low numbers of butterflies trapped on certain days, some surveys ("bad weather days") were omitted from the remainder of the results and analyses that follow. An equal number of samplings at equal number of sample sites are compared. Subsequent to the elimination of data which are considered not suitable for comparison, a dataset of a total of 2438 captures remained. This set of 2438 captures are analysed and culminated in the results which follow in this Chapter. A total of 27 species were captured during the first study period from June 2008-May 2009, whilst 18 species were captured during the second study period from March-May 2010 (Tables 3, 4).

Sampling adequacy at both forests are assessed with the aid of species accumulation curves. The species accumulation curve for the first study period shows that after an initial rapid rate of increase in number of species, the species accumulation drops quickly. For the next fifteen days the curve reaches a plateau and remains constant at 22 species. At day 24 there is a slow increase in the capture of additional butterfly species and appears to level out once more from day 27 to day 31. However at day 32 there is once again an upward trend. Some species only arrive at certain seasons during the year. The species accumulation curve in general approaches an asymptote or at least the rate of increase drops considerably after a few days of sampling (Fig. 10). Overall those species captured after the initial rapid rate are species that are inevitably rarely trapped.

During the second study period in March-May 2010, the species curve starts with 9 species and reaches 18 species in 5 days (Fig. 11). The slope of species increase is significantly less than the initial rapid rate of increase in species numbers during the June 2008 – May 2009 period (Fig. 11).

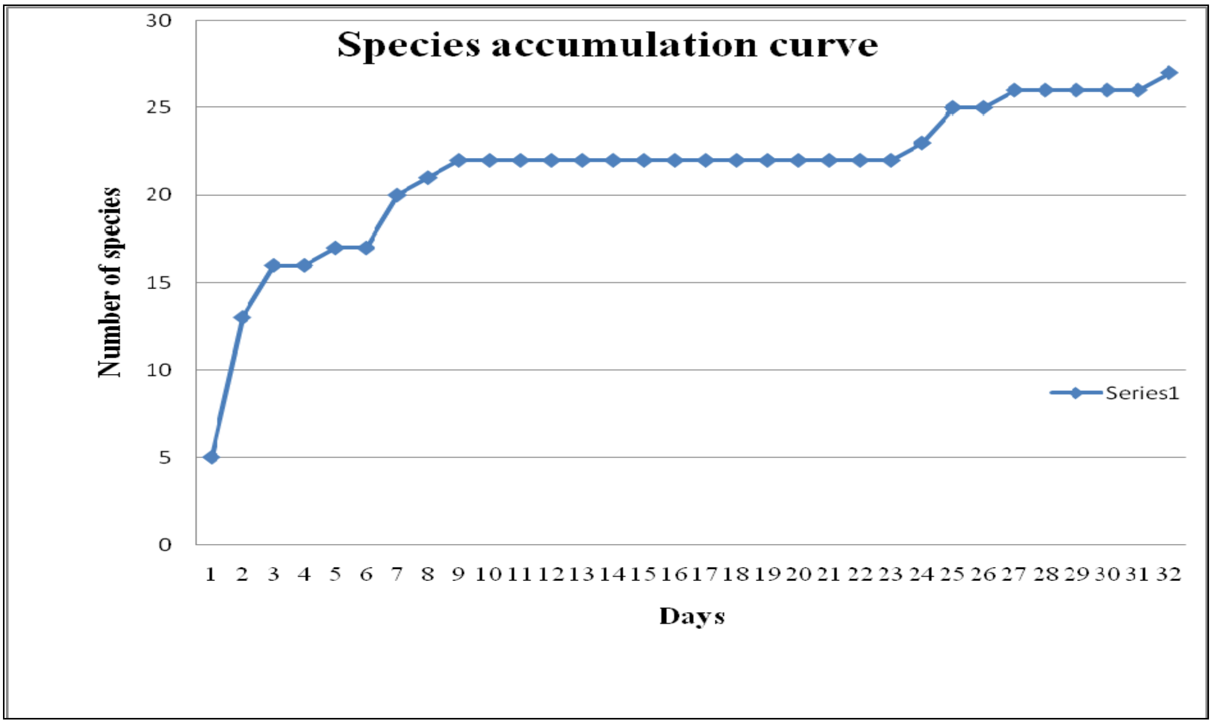


Fig. 10. Species accumulation curve for the number of species recorded with baited trap during the period June 2008 - May 2009.

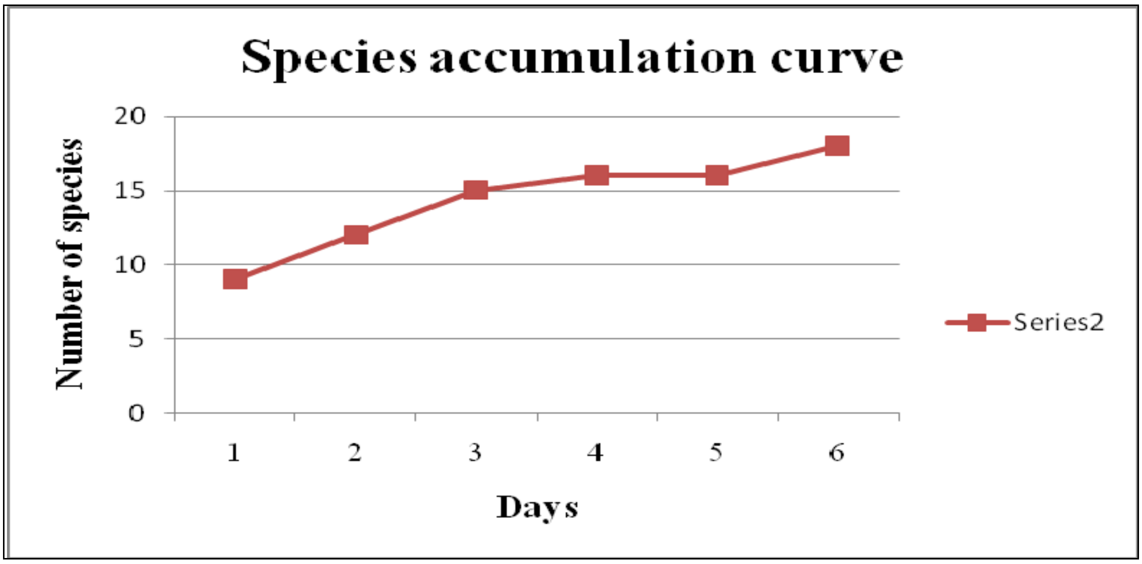


Fig. 11. Species accumulation curve for the fruit-feeding butterfly species recorded with baited traps at Dlinza and Entumeni forests for the period March-May 2010 (autumn).

During the first study period of twelve months (June 2008 – May 2009) consisting of 160 hours of sampling per baited trap, 1711 butterflies belonging to 27 species representing 5 subfamilies of Nymphalidae were trapped **(**Table 3). 25 species (777 individuals) were captured at Entumeni and 20 species (934 individuals) at Dlinza, with 18 species in common between both forest patches. Overall the most species rich and abundant subfamily was Charaxinae (9 species, 803 individuals), followed by Biblidinae (6, 351), Satyrinae (5, 508), Limenitinae (4, 39), Nymphalinae (3, 10).

During the follow-up surveys of three months during autumn of 2010 (March – May 2010) consisting of 30 hours of sampling per baited trap, 727 butterflies belonging to 18 species representing 5 subfamilies of Nymphalidae were trapped (Table 4). 17 species (468 individuals) were trapped at Entumeni and 15 species (259 individuals) were trapped at Dlinza, with 14 species in common between the forest patches. The most species rich and abundant subfamily was once again Charaxinae (8 species, 394 individuals), followed by Biblidinae (4, 70), Satyrinae (3, 255), Limenitinae (2, 7), Nymphalinae (1,1).

Table 3. Representation of subfamilies, species, total abundances and total number of species of fruit-feeding butterflies recorded with baited traps at Dlinza and Entumeni forests during the first study period June 2008-May 2009.

Species	Subfamily	Abundance	
		Dlinza	Entumeni
Melanitis leda (Linnaeus, 1758)	Satyrinae	-	1
Paralethe dendrophilus indosa (Trimen, 1879)	Satyrinae	10	10
Bicyclus anynana anynana (Butler, 1879)	Satyrinae	3	-
Bicyclus safitza safitza (Westwood, 1851)	Satyrinae	273	205
Heteropsis perspicua perspicua (Trimen, 1873)	Satyrinae	2	4
Junonia terea elgiva (Hewitson, 1864)	Nymphalinae	-	2
Precis tugela tugela (Trimen, 1879)	Nymphalinae	2	2
Catacroptera cloanthe cloanthe (Stoll, 1781)	Nymphalinae	1	3
Byblia anvatara acheloia (Wallengren, 1857)	Biblidinae	-	2
Byblia ilithyia (Drury, 1773)	Biblidinae	-	2
Eurytela dryope angulata (Aurivillius, 1899)	Biblidinae	45	25
Eurytela hiarbas angustata (Aurivillius, 1894)	Biblidinae	89	172
Sevenia boisduvali boisduvali (Wallengren, 1857)	Biblidinae	5	10
Sevenia natalensis (Boisduval, 1847)	Biblidinae	-	1
Neptis laeta (Overlaet, 1955)	Limenitidinae	1	-
Neptis saclava marpessa (Hopffer, 1855)	Limenitidinae	-	1
Cymothoe coranus coranus (Grose-Smith, 1889)	Limenitidinae	16	18
Pseudacraea lucretia tarquinea (Trimen, 1868)	Limenitidinae	1	2
Charaxes brutus natalensis (Staudinger, 1885)	Charaxinae	50	53
Charaxes candiope candiope (Godart, 1824)	Charaxinae	129	111
Charaxes cithaeron cithaeron (Felder & Felder, 1859)	Charaxinae	137	31
Charaxes druceanus druceanus (Butler, 1869)	Charaxinae	8	4
Charaxes ethalion ethalion (Boisduval, 1847)	Charaxinae	25	45
Charaxes jahlusa argynnides (Westwood, 1864)	Charaxinae	-	1
Charaxes varanes varanes (Cramer, 1777)	Charaxinae	90	34
Charaxes xiphares penningtoni (Van Son, 1953)	Charaxinae	39	29
Charaxes zoolina zoolina (Westwood, 1850)	Charaxinae	8	9
Total abundance		934	777
Total number of species		20	25

Table 4. Representation subfamilies, species, total abundances and total number of species of fruit-feeding butterflies recorded with baited traps at Dlinza and Entumeni forest during the second study period March-May 2010.

Species	Subfamily	Abundance	
		Dlinza	Entumeni
Melanitis leda	Satyrinae	1	1
Paralethe dendrophilus indosa	Satyrinae	7	6
Bicyclus safitza safitza	Satyrinae	91	149
Catacroptera cloanthe cloanthe	Nymphalinae	-	1
Byblia anvatara acheloia	Biblidinae	-	1
Eurytela dryope angulata	Biblidinae	2	3
Eurytela hiarbas angustata	Biblidinae	18	45
Sevenia moranti moranti	Biblidinae	1	-
Cymothoe coranus coranus	Limenitidinae	1	5
Pseudacraea lucretia tarquinea	Limenitidinae	-	1
Charaxes brutus natalensis	Charaxinae	16	37
Charaxes candiope candiope	Charaxinae	43	103
Charaxes cithaeron cithaeron	Charaxinae	40	32
Charaxes druceanus druceanus	Charaxinae	2	2
Charaxes ethalion ethalion	Charaxinae	2	41
Charaxes varanes varanes	Charaxinae	13	20
Charaxes xiphares penningtoni	Charaxinae	21	20
Charaxes zoolina zoolina	Charaxinae	1	1
Total abundance		259	468
Total number of species		15	17

Although the richest subfamily was Charaxinae, the species *B. safitza safitza* was the butterfly species which had the highest abundance during both study periods and recorded a relative abundance of 29.5 % (Table 5). The second most abundant species was *C. candiope candiope* (15.8 %) followed by *E. hiarbas angustata* at 13.29 % and *C. cithaeron cithaeron* at 9.85 %. Only 8 species showed high abundances and made large contributions to the overall number of butterflies captured. Thirteen butterfly species recorded very low abundances and were below 10 individuals, while 4 species were only captured once (Table 5).

Table 5. Total abundances and relative abundances (%) of species recorded with baited traps Dlinza and Entumeni forests for both study periods June 2008 - May 2099 and March – May 2010.

SPECIES	TOTAL ABUNDANCE	RELATIVE ABUNDANCE (%)
M. leda	3	0.12
P. dendrophilus	33	1.35
B. anynana	3	0.12
B. safitza safitza	718	29.50
H. perspicua	6	0.25
J. terea elgiva	2	0.08
P. tugela	4	0.16
C. cloanthe	5	0.20
B. anvatara	3	0.12
B. ilithyia	2	0.08
E. dryope	75	3.08
E. hiarbas	324	13.29
S. boisduvali	15	0.61
S. natalensis	1	0.04
N. laeta	1	0.04
N. saclava	1	0.04
C. coranus	40	1.64
P. lucretia	4	0.16
C. brutus natalensis	156	6.40
C. candiope candiope	386	15.84
C. cithaeron cithaeron	240	9.85
C. druceanus druceanus	16	0.66
C. ethalion ethalion	113	4.64
C. jahlusa argynnides	1	0.04
C. varanes varanes	157	6.44
C. xiphares penningtoni	109	4.47
C. zoolina zoolina	19	0.78

At both Dlinza and Entumeni forest patches the highest relative abundance recorded with baited traps was in the Charaxinae, followed by Satyrinae and Biblidinae (Figs 12, 13). There were no species trapped at Dlinza forest from the subfamily Nymphalinae, with only a small representation of 2 % from Limenitidinae, while at Entumeni forest Nymphalinae had a 1 % representation and a marginally higher percentage of Limenitidinae than at Dlinza forest of 3 % (Figs 12, 13). The smaller Dlinza forest had a higher percentage of Charaxinae than the larger rural Entumeni forest, while the subfamily Biblidinae had a greater representation at Entumeni forest (Figs 12, 13).

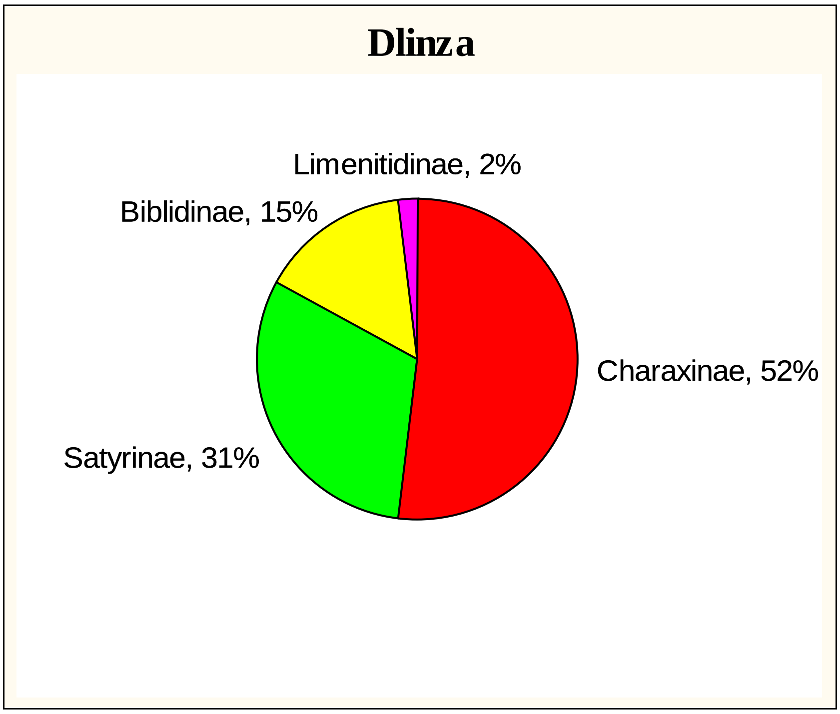


Fig. 12. Subfamily representation of butterfly abundances recorded with baited traps at Dlinza forest during the period June 2008 - May 2009.

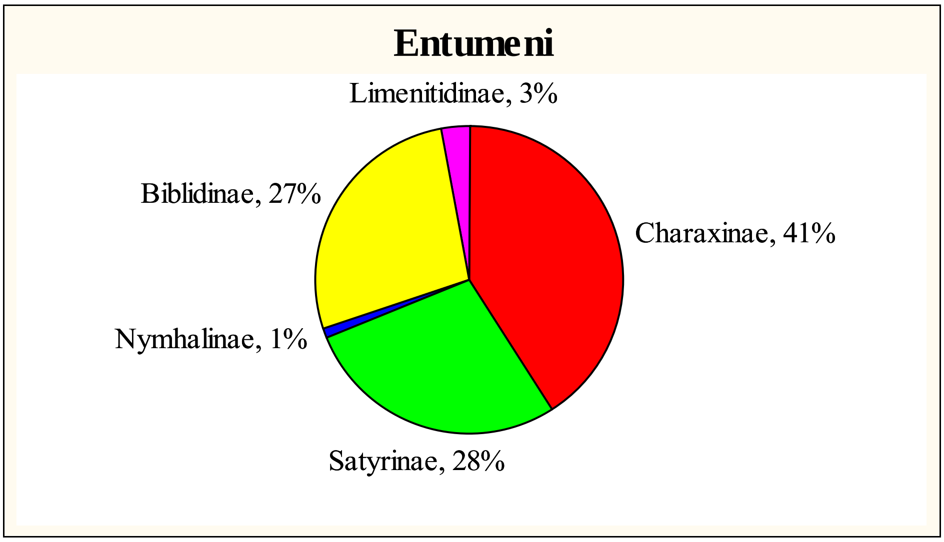


Fig. 13. Subfamily representation of butterfly abundances recorded with baited traps at Entumeni forest during the period June 2008 - May 2009.

Of the 18 Afrotropical Charaxinae species-groups according to Henning (1989), there are 9 represented in South Africa and KwaZulu-Natal, while 7 of these species-groups were found in the study area (Table 6). The *C. etheocles* and *C. jasius* groups are the best represented in South Africa and KwaZulu-Natal in terms of numbers of species. Highest numbers of species have been found in the *C. jasius* and *C. tiridates* groups at Dlinza and Entumeni forests (Table 6).

Table 6. Summary of the Charaxinae species-groups for the Afrotropical region indicating numbers of species for Africa, South Africa, KwaZulu-Natal, and number of species trapped at Dlinza and Entumeni forests. Literature sources: Henning (1989), Pringle, Henning & Ball (1994).

***Charaxes* species-groups**	**Afrotropical**	**RSA**	**KZN**	**Dlinza and Entumeni**
varanes	8	1	1	1
jasius	20	5	4	2
acraeoides	2	-	-	-
zingha	1	-	-	-
etesipe	5	2	2	-
cynthia	6	1	1	-
nobilis	3	-	-	-
hadrianus	2	-	-	-
etheocles	62	6	4	1
lucretius	4	-	-	-
tiridates	18	3	2	2
jahlusa	1	1	1	1
candiope	3	1	1	1
pleione	2	-	-	-
zoolina	2	1	1	1
eupale	4	-	-	-
nichetes	1	-	-	-
laodice	6	-	-	-

4.1.3 General seasonal patterns

During the first 12 month study period June 2008-May 2009, 1004 butterflies were trapped during autumn (March-May), 265 during winter (June-August), 244 during spring (September-November), and 198 during summer (December-February) (Fig. 14). The number of individuals trapped during autumn was significantly higher than winter ($p = 0.000387$; $t = 4.181$, d.f. = 22) (Fig. 14). The number of individuals trapped during autumn represented approximately 58 % of the total abundance, while winter made up 15 %, spring 14 %, and summer 11 % (Fig.14).

With regard to the number of species trapped during the different seasons**,** the highest number of species were recorded during autumn (March-May) and winter (June-August) at 21 species, followed by spring (September-November) which recorded 17 species, and with summer (December-February) having the lowest value of 15 species (Fig. 15).

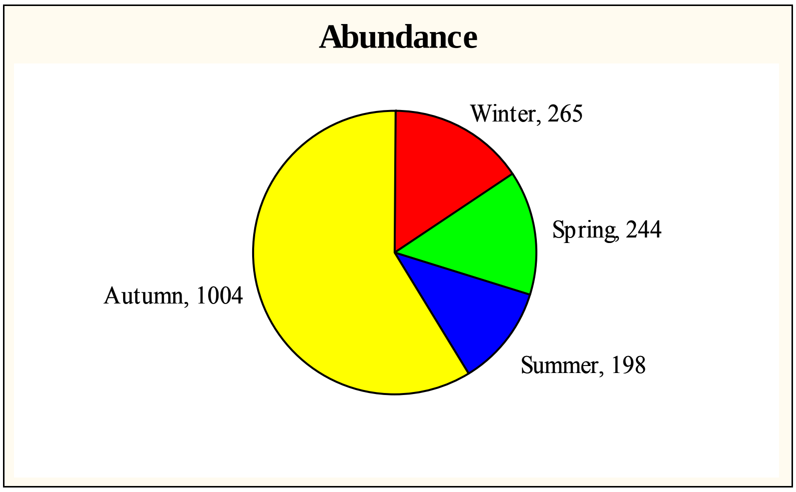


Fig. 14. Total butterfly abundance as recorded by baited traps for each season at the Dlinza and Entumeni forests for the first study period June 2008-May 2009.

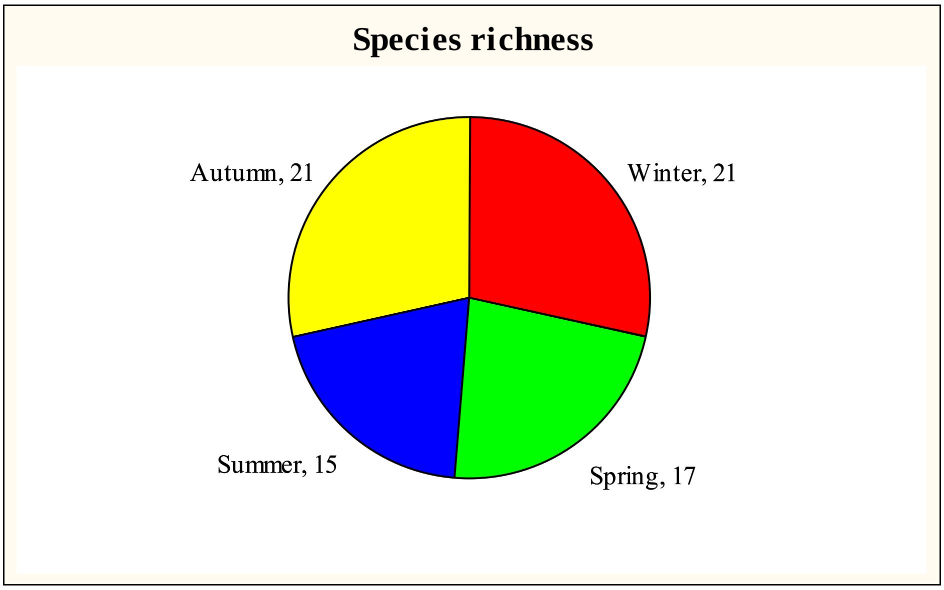


Fig. 15. Number of butterfly species recorded with baited traps for each season at Dlinza and Entumeni forests for the first study period June 2008-May 2009.

During winter, an overall higher number of individuals were trapped at Entumeni forest when compared to the smaller Dlinza forest. However during spring and summer Dlinza forest had a higher abundance than Entumeni forest (Fig. 16). The number of individuals trapped at Dlinza forest during spring was significantly higher than at Entumeni ($p = 0.0099$; $t = 3.169$, d.f. = 10) (Fig. 16). An equal number of butterflies were trapped at the two forests during autumn 2009 (Fig. 16). During the second study period of autumn 2010, a higher abundance of fruit-feeding butterflies was recorded at Entumeni forest in comparison to Dlinza forest ($p = 0.148$; $t = -1.567$, d.f. = 10) (Fig. 16).

With regard to species richness a higher number of species were recorded at Entumeni forest for winter, summer, and autumn, however during spring an equal number of species were trapped at the two nature reserves (Fig. 17). During the second study period of autumn 2010 a higher species richness was observed at Entumeni forest compared to Dlinza forest (Fig. 17).

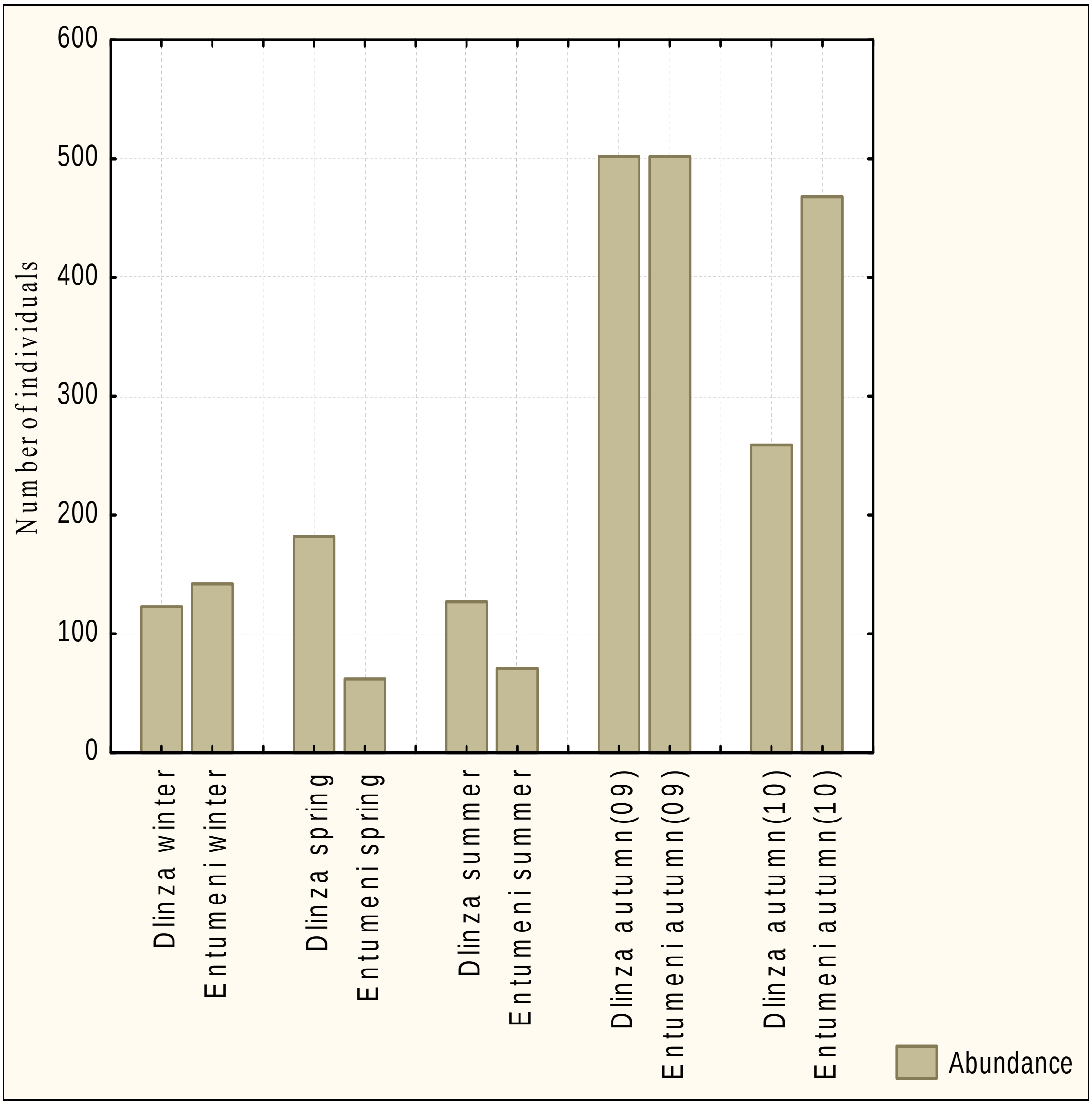


Fig. 16. Seasonal comparison of abundances recorded with baited traps at Dlinza and Entumeni forests for both study periods of June 2008-May 2009 and March-May 2010 ("autumn 2010").

Winter: June-August
Spring: September-November
Summer: December-February
Autumn: March-May

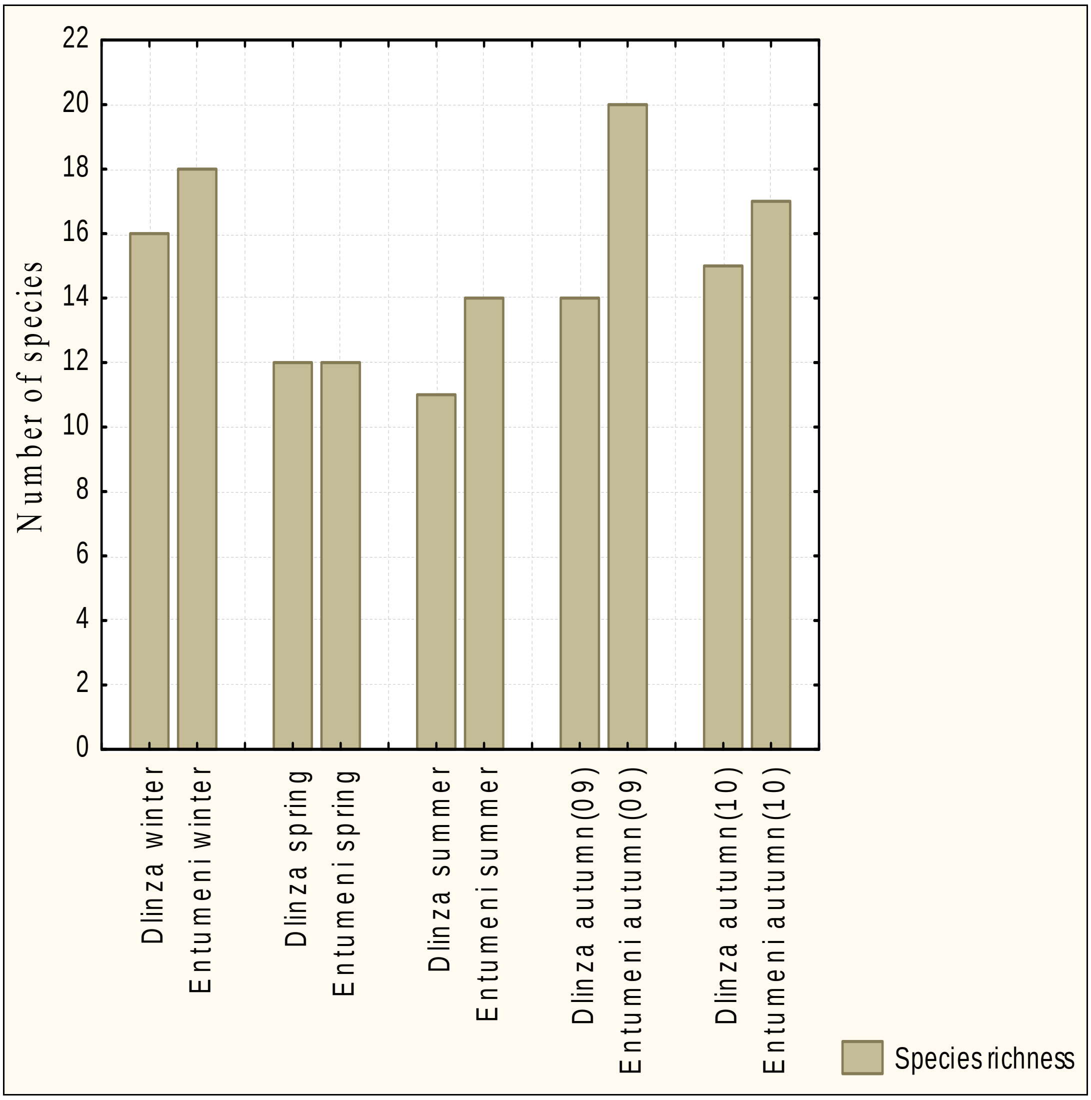


Fig. 17. Seasonal comparison of total number of species recorded with baited traps at Dlinza and Entumeni forests for both study periods of June 2008-May 2009 and March-May 2010.

Winter: June-August
Spring: September-November
Summer: December-February
Autumn: March-May

4.2 Assemblage structure

Total abundances, species richness and diversities of the two forests are compared, but because of the strong seasonal influences to abundances, species richness and diversity which are noticeable in the previous section (4.2 General seasonal patterns) much of the comparisons take place in context of seasons.

4.2.1 Abundance

During the first study period (June 2008-May 2009) a higher number of individuals in total was recorded at the Dlinza forest when compared to the Entumeni forest. During the second study period (March-May 2010) a lower total abundance was recorded for Dlinza compared to Entumeni (Table 3, Table 4). During March-May 2009 and March-May 2010 an equal total abundance was recorded for both forests in autumn 2009 but a higher total abundance at Entumeni in autumn 2010 (Figs 18,19).

Abundances differed considerably between forest interiors and edges of both the Dlinza and Entumeni forests. For the period June 2008-May 2009, Dlinza forest had a higher abundance at the forest edge when compared to the forest interior for all four seasons with the difference greater during autumn ($p = 0.0146$) (Fig 18). Abundances at the Entumeni forest displayed a similar trend as Dlinza forest with a higher abundance at the forest edge for winter, spring, and autumn, with the largest difference during autumn ($p = 0.0263$) (Fig 18). However during summer the forest interior at Entumeni had a higher abundance when compared to the forest edge (Fig. 18). During the second study period March-May 2010 both forest patches had higher abundances of butterflies at the forest edge in comparison to the forest interior (Fig. 18). Mean abundances of fruit-feeding butterflies were higher at the forest edges than the forest interiors (Fig. 19). There was higher variation at the smaller Dlinza forest, than at Entumeni forest (Fig 19).

A comparison of forest interiors between patches, showed Dlinza forest having a consistently higher number of individuals for winter, spring, and summer (Fig 18), however during autumn Entumeni forest had a higher number in comparison to Dlinza forest interior (Fig. 18). The forest edge at Dlinza was higher in abundance than Entumeni forest edge for spring, summer, and autumn (Figs 18), with higher numbers at Entumeni forest edge for winter (Fig. 18). However Entumeni forest interior once again had a higher mean abundance when compared to Dlinza forest interior. Data indicated a greater variation in abundance than the first study ($p = 0.125$; $t = -1.931$, d.f. = 4) (Figs 21b).

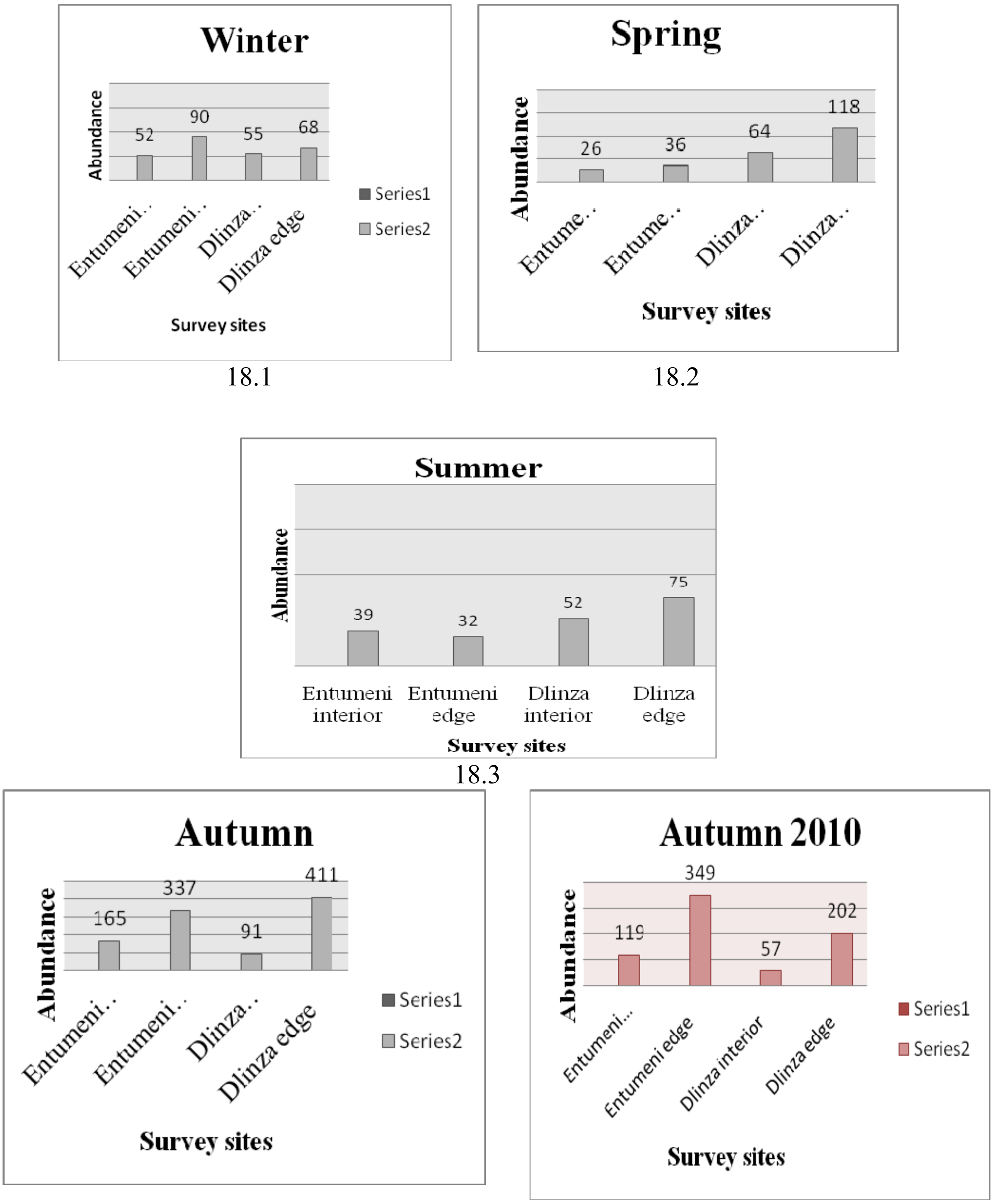
When comparing the difference in abundance at forest edge and interior between landscapes, the smaller Dlinza forest had a higher abundance at the forest edge, however a higher number of butterflies were sampled at Entumeni forest interior than at Dlinza forest interior in autumn

(Fig 18). During the second study period when comparing forest edge and forest interior between landscapes, there was a different trend to the first study period. Entumeni forest edge now recorded a significantly higher abundance in comparison to Dlinza forest edge (p = 0.0477; t = 2.821, d.f. = 4 (Fig. 21 a).

During the second study period of autumn 2010 a different result was found when comparing the number of butterflies at the forest edge of the two reserves. The butterfly abundance was found to be higher at Entumeni forest edge than at Dlinza forest edge, however the number of individuals was still higher at Entumeni forest interior in comparison to Dlinza forest interior (Fig. 18).

At both reserves the forest edge had a higher mean abundance when compared to the forest interior, with the difference at the smaller urban Dlinza forest significant (p = 0.0394; t = 3.012, d.f.= 4), while at the larger rural Entumeni forest reserve there was lower variation (p = 0.0653; t = -2.520, d.f. = 4) (Fig. 19). When comparing the mean butterfly abundance at the forest edge between forest reserves, a higher abundance was found at Dlinza forest edge than Entumeni forest edge (p = 0.224; t = 1.436, d.f. = 4) (Fig. 20 a). There was low variation in mean abundance between the interior of the two forests (p = 0.854; t = -0.195, d.f. = 4), with Entumeni forest being marginally higher than Dlinza forest (Fig. 20 b).

When comparing the butterfly abundance at individual survey sites at Dlinza and Entumeni forests, the trend was a higher abundance at forest edge survey sites for both study periods (Tables 7, 8). The only exception being EE3 of which a lower abundance of butterflies was observed compared to EI2 during the first study period (Table 7). An interesting observation was that DI1 which was the only survey point located in the canopy had a relatively low abundance when compared with other survey sites in the forest (Tables 7, 8). Two forest interior survey sites, DI3 and EI2 recorded the highest number of individuals when compared to the other interior survey sites (Tables 7, 8).



18.1

18.2

18.3

18.4

18.5

Fig.18. Fruit-feeding butterfly abundances recorded with baited traps at Dlinza and Entumeni forest interiors and edges for both study periods June 2008-May 2009 and March-May 2010.

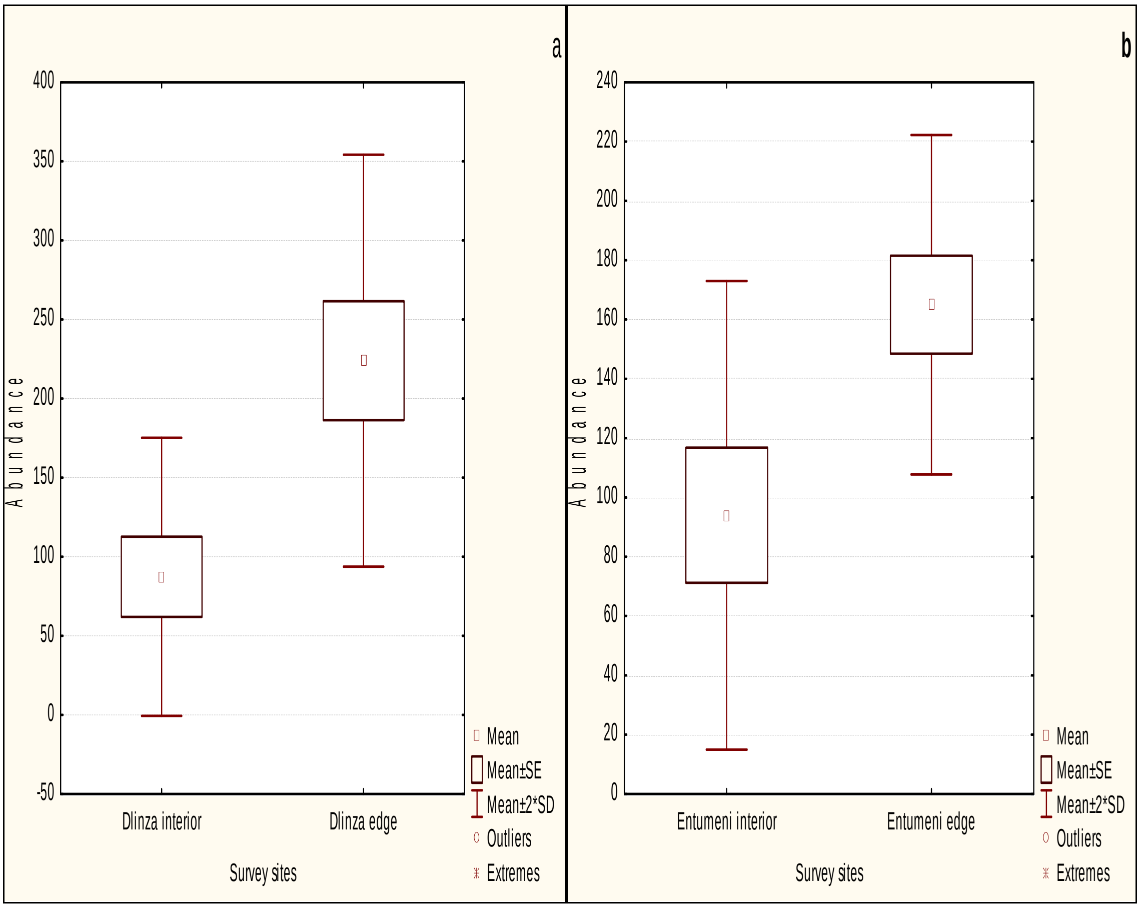


Fig. 19. Box and whisker plots showing mean abundance of fruit-feeding butterflies recorded with baited traps at Dlinza (a) and Entumeni (b) forest interior and edge for the period June 2008-May 2009.

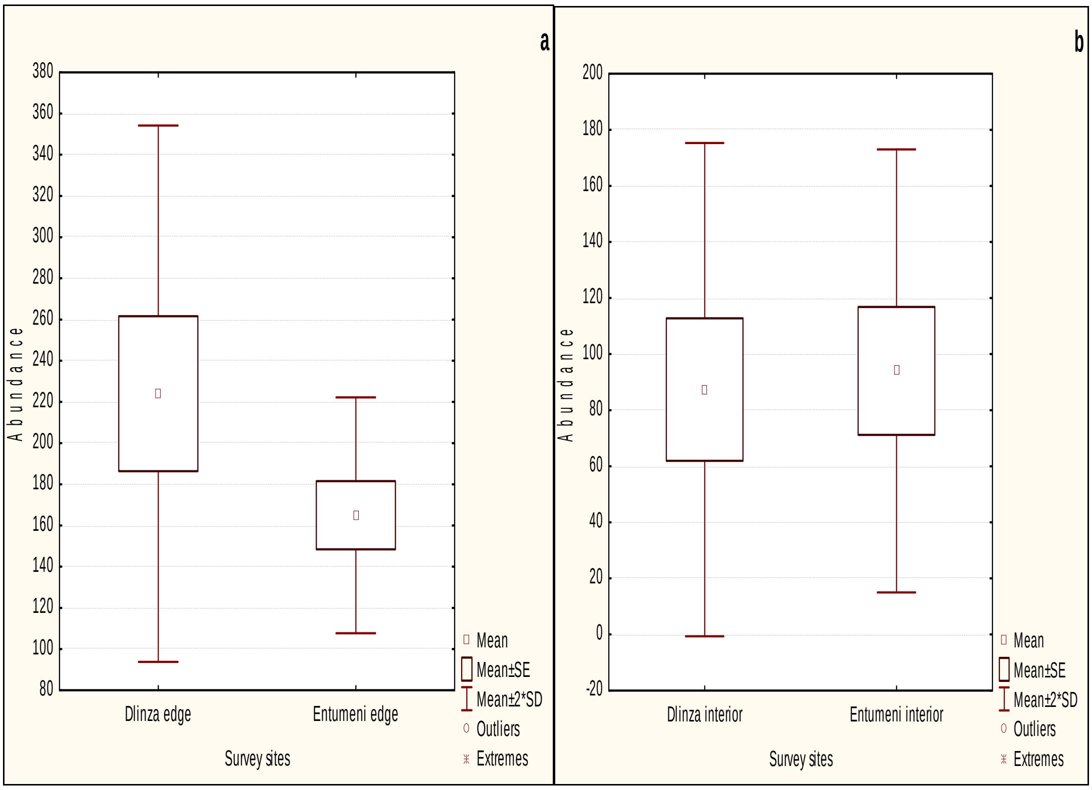


Fig. 20. Box and whisker plots showing mean abundance of fruit-feeding butterflies recorded with baited traps at Dlinza and Entumeni forest edge (a) and forest interior (b) for the period June 2008-May 2009.

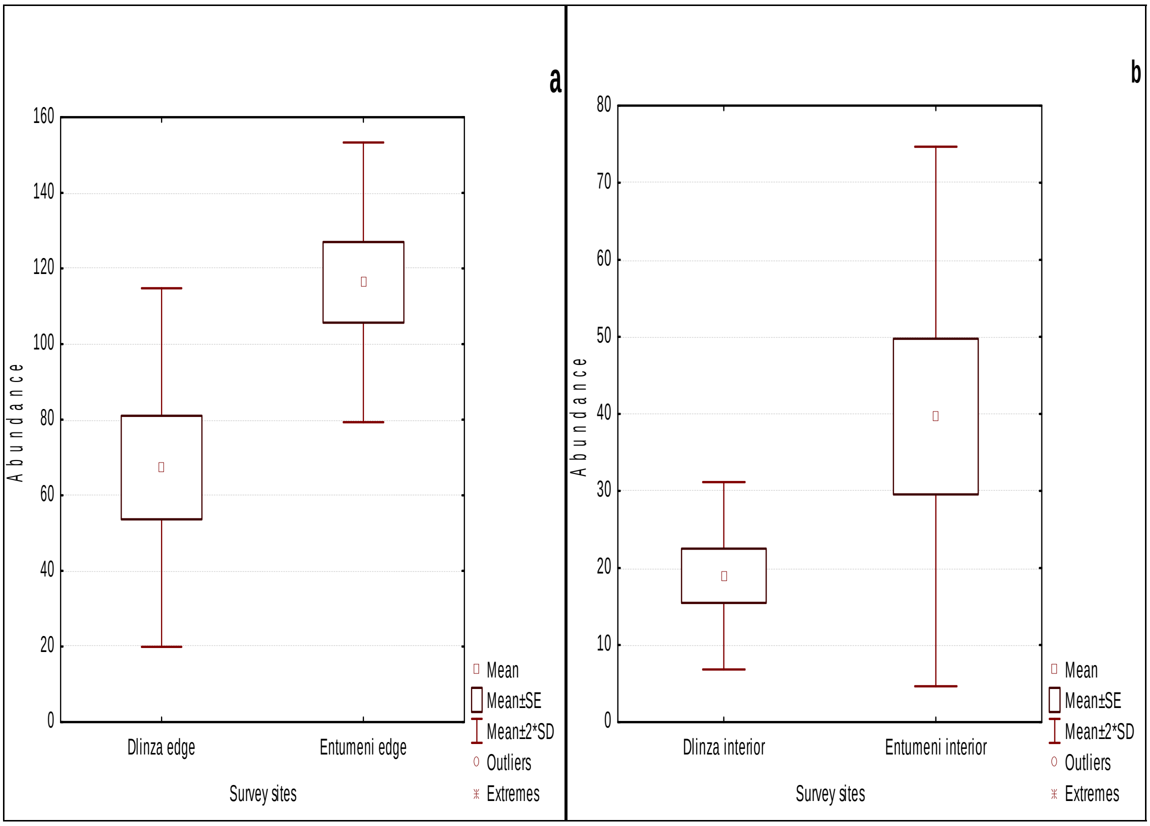
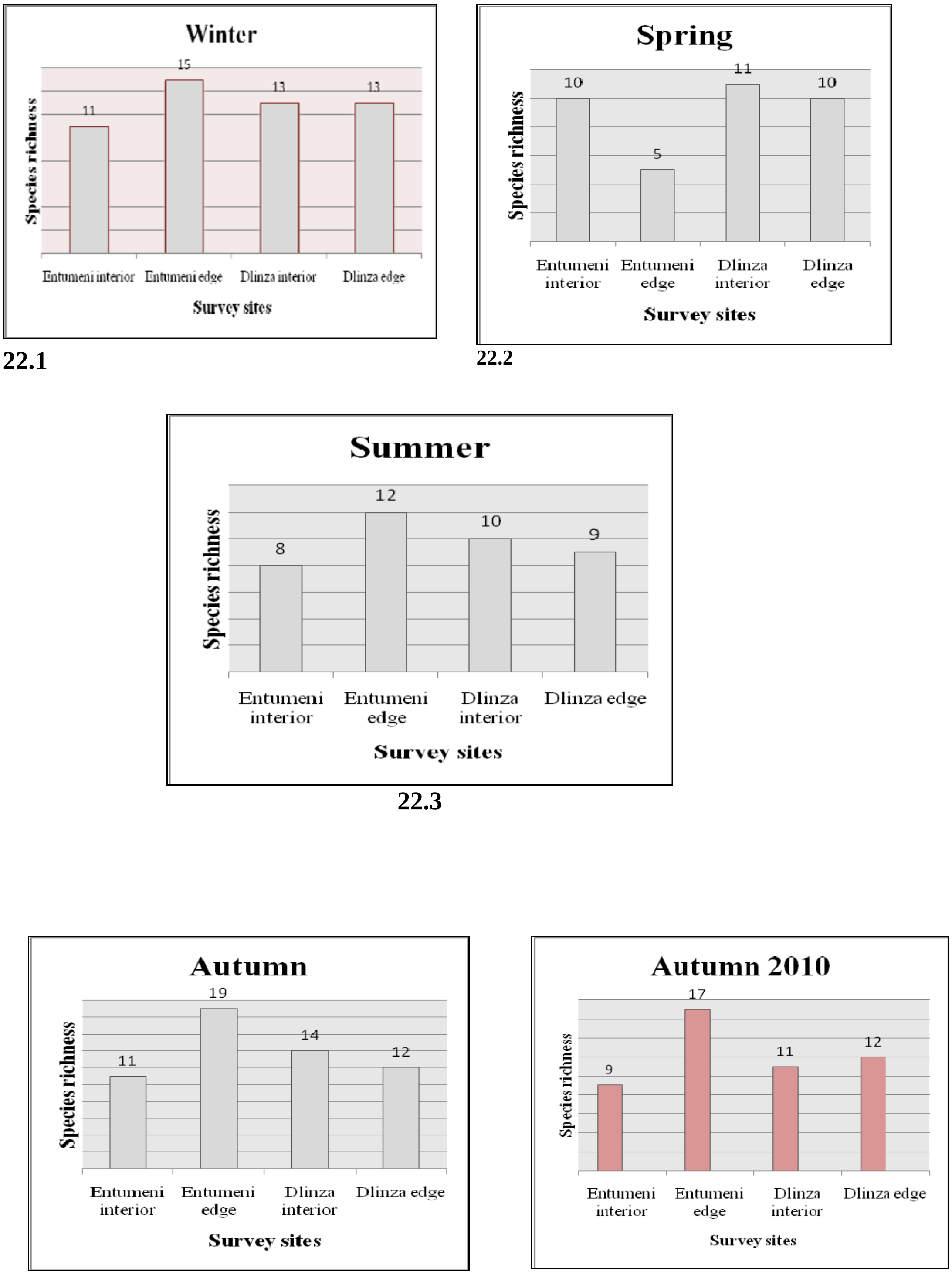


Fig. 21. Box and whisker plots showing mean abundance of fruit-feeding butterflies recorded with baited traps at Dlinza and Entumeni forest edge (a) and forest interior (b) for the period March-May 2010 (autumn).

4.2.2 Species richness

During the first study period (June 2008-May 2009) a higher number of species in total was recorded at the Entumeni forest compared to the Dlinza forest. During the second study period (March-May 2010) a similar trend was observed where a higher number of species was recorded for Entumeni compared to Dlinza (Tables 3, 4). No significant difference between the forest remnants in the overall mean species richness (d) index is observed. The larger Entumeni forest was marginally higher in comparison to Dlinza forest ($p = 0.396$; $t = -0.885$, d.f. = 10) (Tables 7, 8). Seasonal variation in the number of species is considerable, adding to the variation around the means.

Number of species and species richness (d) differed considerably between forest interiors and edges of both the Dlinza and Entumeni forest patches. Comparison of the total number of species trapped at the forest interior and forest edge for each season at Dlinza and Entumeni forests showed a higher number of species trapped at Dlinza forest interior in comparison to the forest edge for spring, summer, and autumn, with winter having an equal number of species recorded (Fig 22). At Entumeni the forest edge had a higher number of species for winter, summer, and autumn, however during spring Entumeni forest interior was higher than the forest edge (Fig 22). During the second study period March-May 2010 both Dlinza and Entumeni forests recorded a higher number of species at the forest edge when compared to the forest interior (Fig. 22). Within individual forest patches Dlinza forest had a higher mean species richness (d) index at the interior of the forest in comparison with the forest edge ($p = 0.076$; $t = 2.376$, d.f. = 4) (Fig. 23a), while at Entumeni forest the opposite trend was found, with a significantly higher mean species richness (d) at the forest edge when compared with the forest interior ($p = 0.0087$; $t = -4.791$, d.f.=4) (Fig. 23b).



22.1 **22.2**

22.3

22.4 **22.5**

Fig. 22. Numbers of fruit-feeding butterfly species recorded with baited traps at Dlinza and Entumeni forest interior and edge for all four seasons for the first study period June 2008-May 2009 and the second study period March-May 2010 (autumn).

When comparing the number of butterfly species trapped at the forest interiors between forest patches for each season in 2008/2009, Dlinza forest interior recorded a higher number of species than Entumeni interior for all four seasons (Fig 22). During the second study period March-May 2010 (autumn) the number of species trapped at the forest interior was also higher at the Dlinza forest interior compared to Entumeni interior (Fig. 22). A higher mean species richness (d) was observed for interior of the smaller urban Dlinza forest compared to Entumeni forest interior ($p = 0.078$; $t = 2.358$, d.f. = 4 (Fig. 24b). The species richness (d) at the forest interior between landscapes during the second study period of March-May 2010 (autumn) showed a similar trend to the first study period June 2008-May 2009. Dlinza forest reserve had a higher mean species richness (d) at the forest interior when compared to Entumeni forest interior ($p = 0.132$; $t = 1.887$, d.f. = 4) (Fig. 25b). Variation however, was lower than the previous study period with no significant differences recorded.

When comparing the number of butterfly species trapped at the forest edges between forest patches for each season, Entumeni forest edge had a higher number of species when compared with Dlinza forest edge for winter, summer, and autumn with only spring being higher at Dlinza edge (Fig 22). During the second study period March-May 2010 (autumn) the number of species trapped at Entumeni forest edge was higher than Dlinza forest edge (Fig. 22). A comparison of forest edges between reserves, a significantly higher mean species richness (d) was recorded for the period June 2008-May 2009 at the larger rural Entumeni forest edge in comparison to Dlinza forest edge ($p = 0.0108$; $t = -4.502$, d.f. = 4) (Fig. 24a). Species richness (d) of forest edge between Dlinza and Entumeni forests during the second study period of autumn 2010 showed a similar trend to the first study period. A higher mean species richness (d) was recorded for Entumeni forest reserve compared to Dlinza forest edge ($p = 0.163$; $t = -1.706$, d.f. = 4) (Fig. 25a). The variation was however lower than the previous study period with no significant differences recorded.

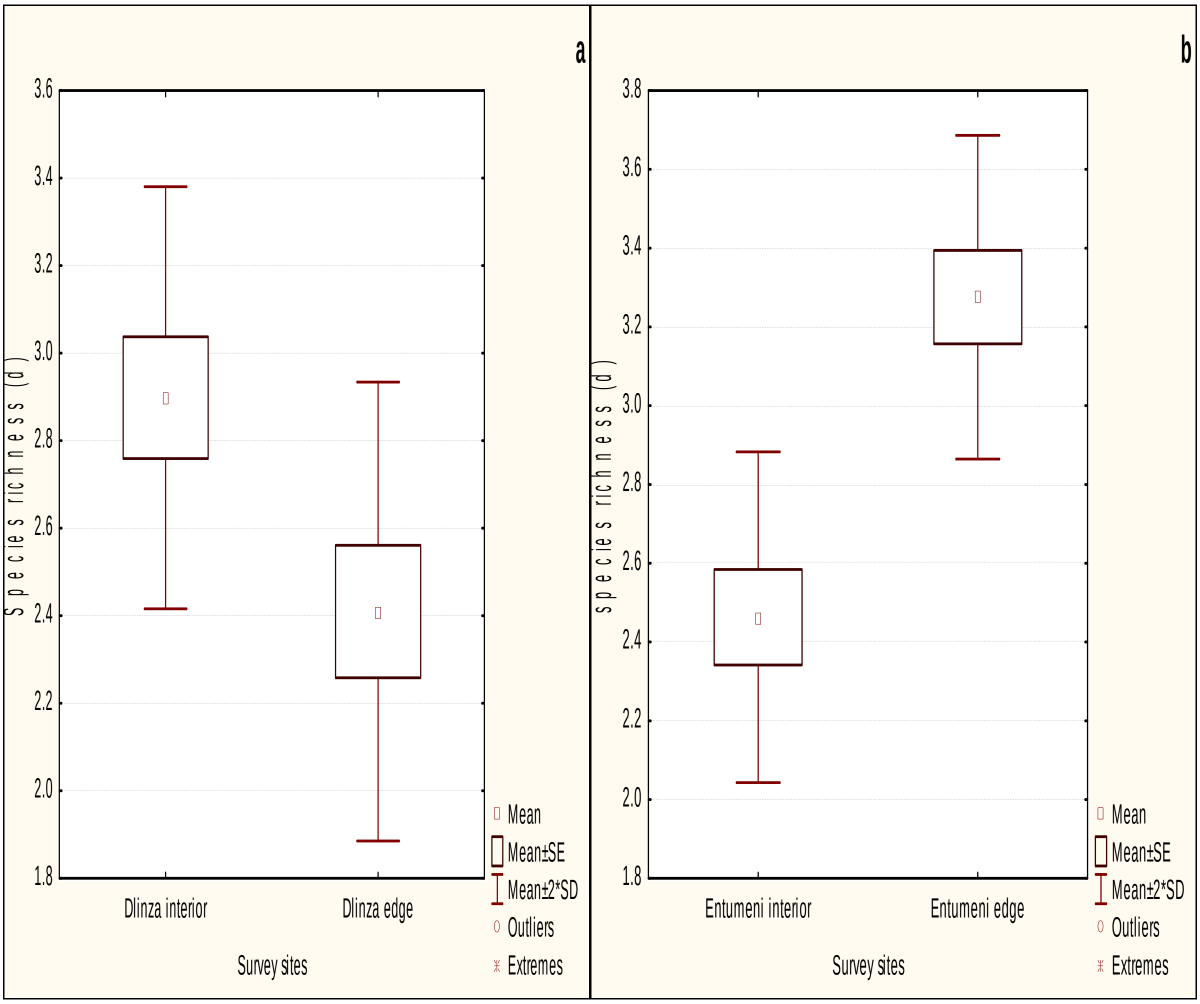


Fig. 23. Box and whisker plots showing mean species richness (d) of fruit-feeding butterflies recorded with baited traps at Dlinza (a) and Entumeni (b) forest interior and edge for the first study period June 2008-May 2009.

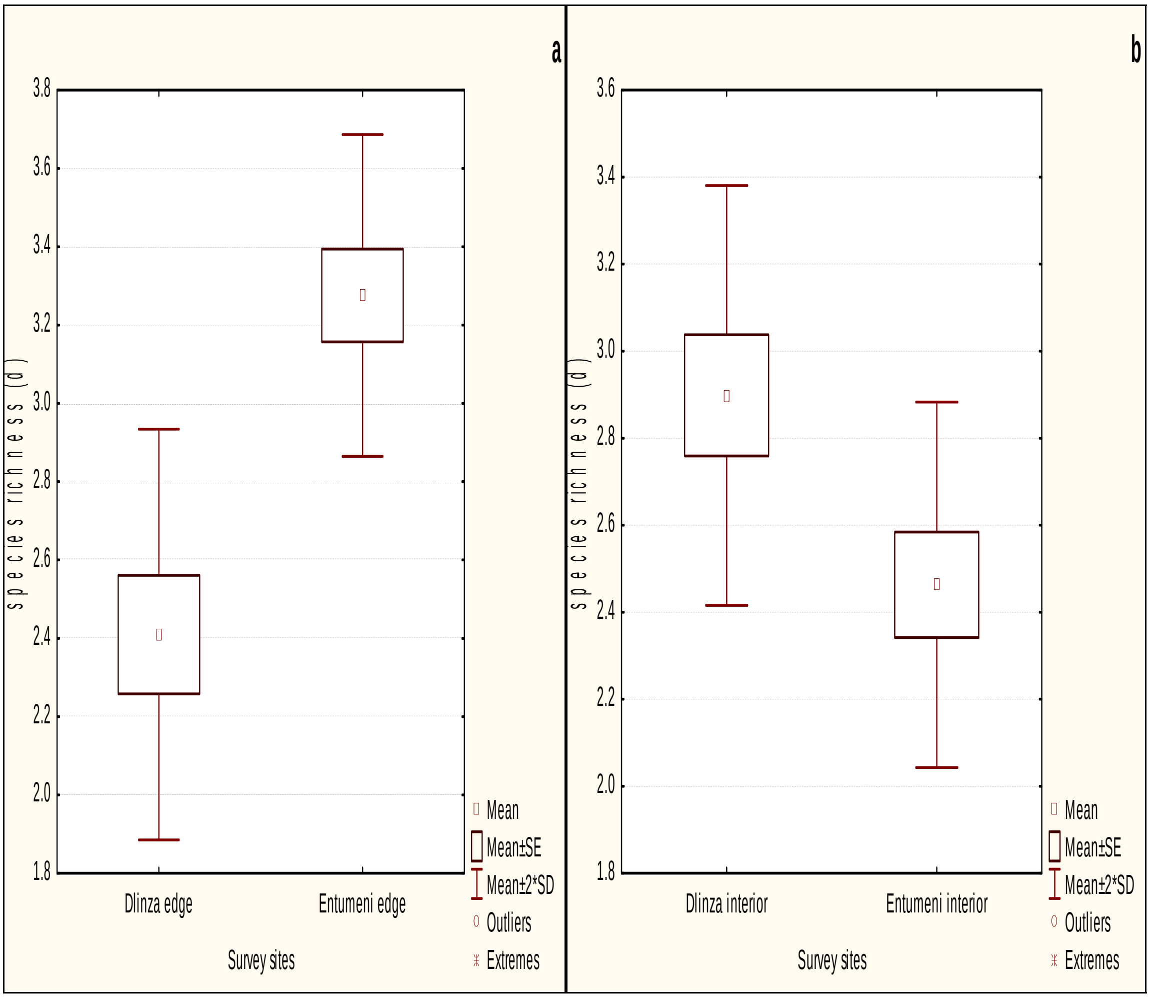


Fig. 24. Box and whisker plots showing mean species richness (d) of fruit-feeding butterflies recorded with baited traps at Dlinza and Entumeni forest edge (a) and forest interior (b) for the first study period June 2008-May 2009.

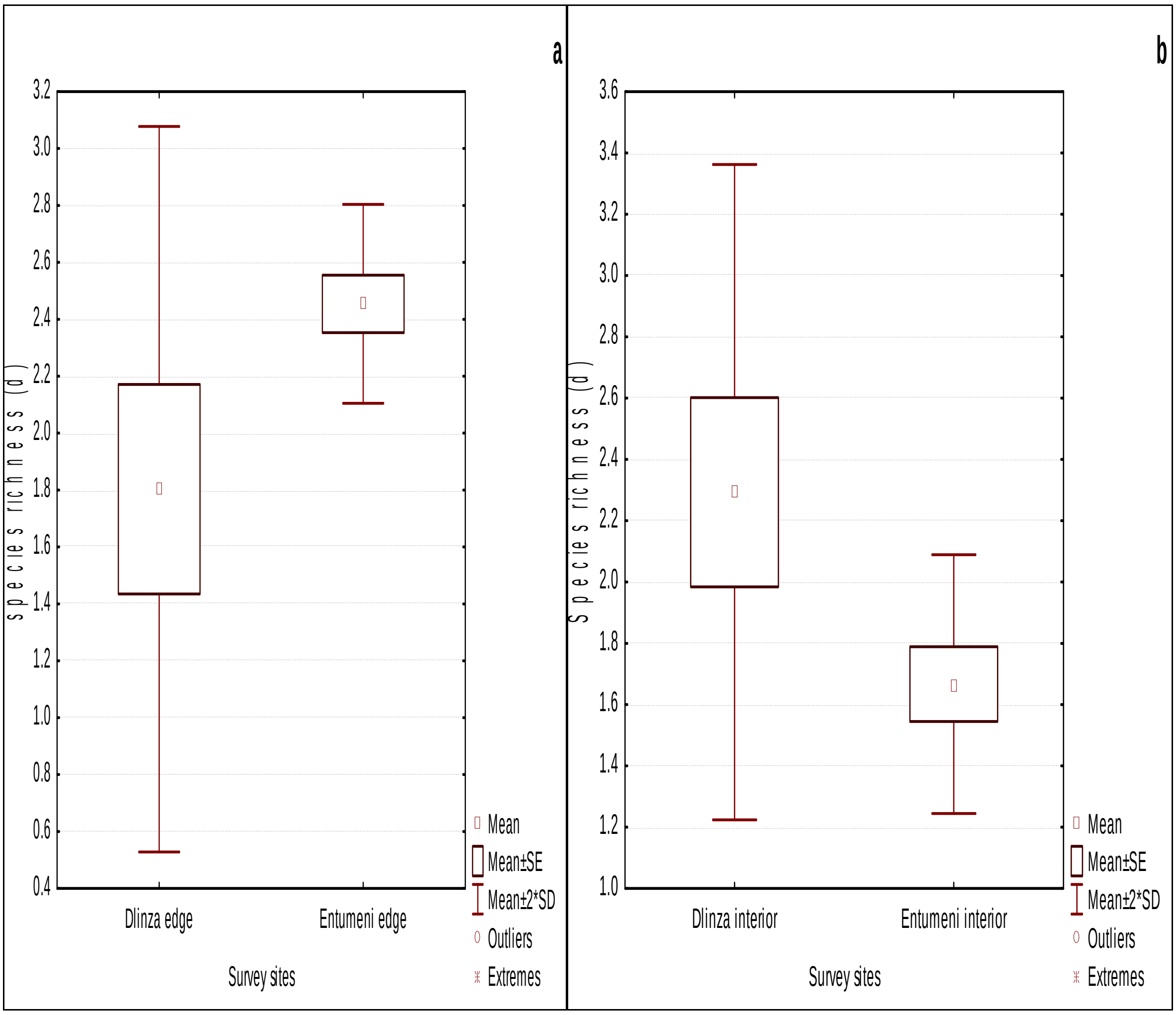


Fig. 25. Box and whisker plots showing mean species richness (d) of fruit-feeding butterflies recorded with baited traps at Dlinza and Entumeni forest edge (a) and interior (b) for the second study period of March-May 2010.

Species richness, both in terms of number of species and species richness index (d) at individual sites followed the average trends presented in previous section. However, some results pertaining to individual sample sites are highlighted. There was low variation in the number of species trapped between individual survey sites at Dlinza forest during the first study period, with DE2 recording the highest number and DE3 the lowest (Table 7). DI1 which was located at the viewing tower in the canopy had similar species richness to the other forest interior survey points (Table 7). At Entumeni forest the trend is higher species richness at forest edge survey points, with EE1 and EE3 having the highest species richness, while at Entumeni forest interior all three sites had an equal number of species (Table 7).

During the second study period of March-May 2010 (autumn), a similar trend was observed as the first study period with Dlinza forest edge points having higher species richness than forest interior points except for DE3 which again had the lowest value (Table 8). At Entumeni forest, the forest edge survey points had the highest species richness.

When comparing the species richness (d) index at individual survey points for the first study period the trend at Dlinza forest was a higher species richness (d) index at forest interior survey points except for DE2 which had a higher value than DI3 (Table 7). DI1 which was located in the canopy had the highest species richness (d) index compared to all the Dlinza forest survey points (Table 7). At Entumeni forest all three forest edge survey points recorded a higher species richness (d) index in comparison to forest interior survey points (Table 7).

During the second study period March-May 2010 (autumn) two sample sites DE1 and DE2 at Dlinza forest edge showed relatively high species richness (d) values, however DI1 once again had the highest species richness (d) value when compared to all the other Dlinza forest survey points (Table 8). At Entumeni forest edge survey points were higher than forest interior survey points (Table 8).

Table 7. Summary of assemblage structure indices of fruit-feeding butterflies recorded with baited traps at Dlinza and Entumeni forest reserves for the first study period June 2008- May 2009. Number of species, abundance, species richness (d), and Shannon diversity indices (H') for the twelve sample sites are included.

Sample point	Number of species(S)	Abundance (N)	Richness index (d)	Evenness(J)	Shannon Diversity index (log10)	l-Lambda
DI1	14	65	3.114	0.8960	1.0270	0.901
DI2	13	59	2.943	0.8297	0.9242	0.8539
DI3	14	138	2.638	0.7772	0.8908	0.8399
DE1	14	266	2.328	0.7478	0.8571	0.8112
DE2	16	257	2.703	0.7786	0.9376	0.8497
DE3	12	149	2.198	0.7843	0.8465	0.8067
EI1	12	78	2.525	0.8365	0.9027	0.8488
EI2	12	139	2.229	0.7558	0.8157	0.7976
EI3	12	65	2.635	0.9097	0.9817	0.8899
EE1	18	180	3.274	0.7602	0.9542	0.841
EE2	17	183	3.071	0.6923	0.8518	0.7893
EE3	18	132	3.482	0.7636	0.9585	0.8407

Table 8. Summary of assemblage structure indices of fruit-feeding butterflies recorded with baited traps at Dlinza and Entumeni forest reserves for the second study period March-May 2010. Number of species, abundance, species richness (d), and Shannon diversity indices (H') for the twelve sample sites are included.

Sample point	Number of species(S)	Abundance (N)	Richness index (d)	Evenness (J)	Shannon diversity index (H)	l-Lambda
DI1	9	16	2.885	0.9315	0.8889	0.9083
DI2	6	15	1.846	0.8856	0.6891	0.8095
DI3	8	26	2.148	0.8738	0.7891	0.84
DE1	11	89	2.228	0.8217	0.8557	0.843
DE2	10	71	2.111	0.8014	0.8014	0.7952
DE3	5	42	1.07	0.7036	0.4918	0.5842
EI1	6	22	1.618	0.916	0.7128	0.8225
EI2	7	57	1.484	0.6336	0.5354	0.5877
EI3	8	40	1.898	0.7604	0.6867	0.7577
EE1	14	135	2.65	0.7705	0.8831	0.8411
EE2	12	116	2.314	0.8359	0.9021	0.858
EE3	12	98	2.399	0.7201	0.7771	0.7709

4.2.3 Diversity

Mean Shannon diversity (H) indices between forest patches for the study period June 2008-May 2009, were very similar with a slightly higher mean index being recorded for the Dlinza forest ($p = 0.937$; $t = 0.0814$, d.f. = 10) (Fig. 26). The survey point DI1 which was located at canopy level on the Dlinza forest aerial boardwalk viewing tower stands out as an outlier at Dlinza forest reserve in terms of diversity (Table 7).

The mean Shannon diversity (H') index between forest interior and edge at each reserve was different and showed marked trends. During the study period June 2008-May 2009, Dlinza forest had a higher mean diversity at the forest interior in comparison to the forest edge ($p = 0.252$; $t = 1.34$, d.f. = 4), while at the larger rural Entumeni forest the opposite trend was found with a higher mean diversity at the forest edge in comparison to the forest interior ($p = 0.735$; $t = -0.362$, d.f. = 4) (Fig. 27). The mean evenness (J) index at Dlinza forest interior was higher when compared to the forest edge (0.834, 0.770), while at Entumeni forest the mean evenness (J) index was marginally higher at the forest interior in comparison to the forest edge (0.834, 0.739) (Table 7).

A comparison of the species diversity of forest interior between forest patches showed no significant differences with the Dlinza forest having a marginally higher mean diversity index at the forest interior in comparison to Entumeni interior ($p = 0.495$; $t = 0.749$, d.f .= 4) (Fig. 28b). During the second study period March-May 2010 (autumn), a comparison of forest edge and forest interior between patches was similar to the previous study. Diversity was once again higher at Dlinza forest interior in comparison to Entumeni interior ($p = 0.146$; $t = 1.803$, d.f.= 4), with no statistically significant differences recorded (Fig 29).

A comparison of the species diversity of forest edge between forest patches showed no significant differences with the diversity at Entumeni forest edge higher than Dlinza forest edge ($p = 0.415$; $t = -0.909$, d.f. = 4) (Fig. 28a). During the second study period March – May 2010 diversity was once again higher at Entumeni forest edge when compared to Dlinza forest edge ($p = 0.314$; $t = -1.150$, d.f.= 4), with no statistically significant differences recorded (Fig 29a).

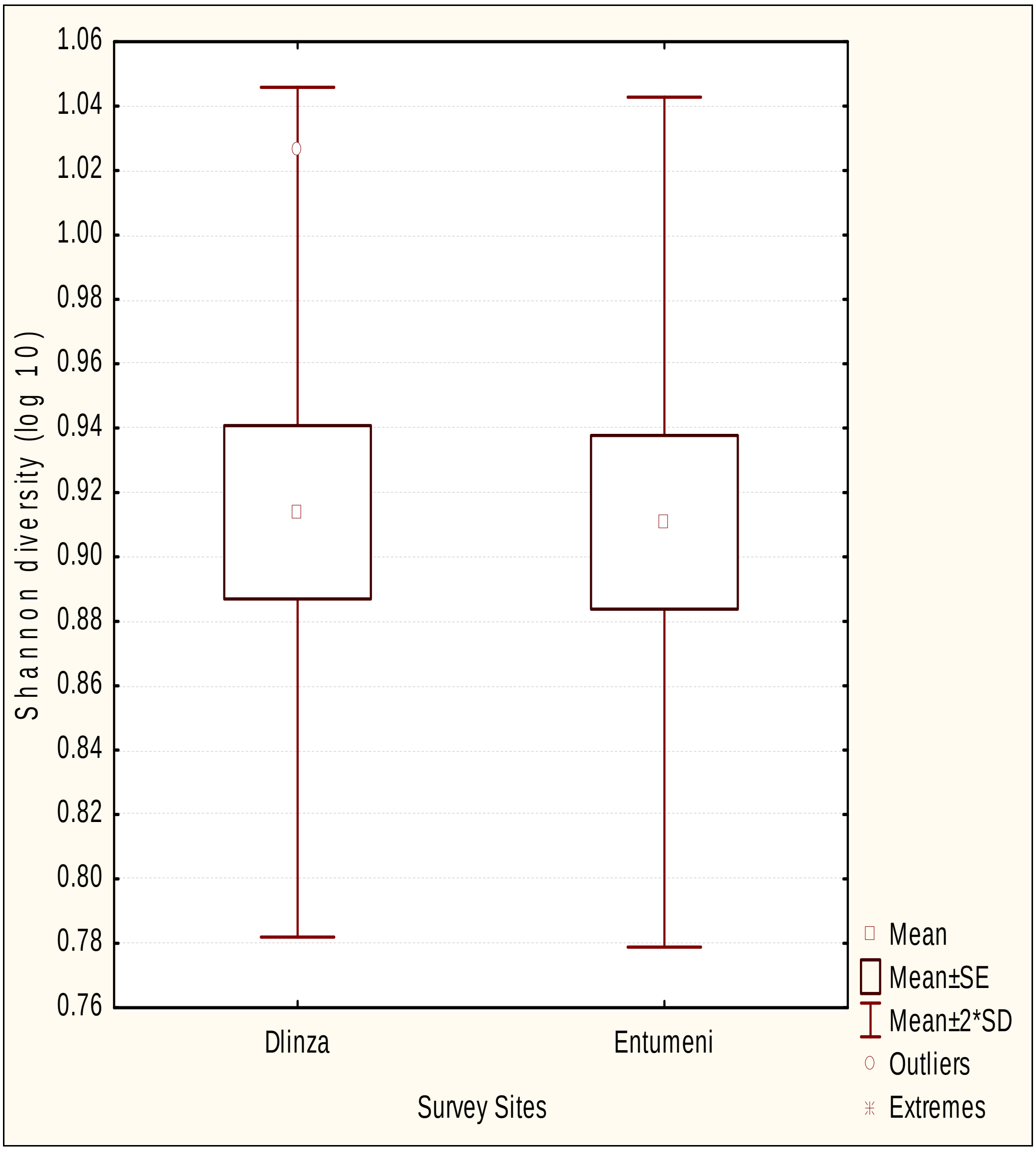


Fig. 26. Box and whisker plots showing mean overall Shannon diversity (H') of fruit-feeding butterfly assemblages recorded with baited traps at Dlinza and Entumeni forest for the study period June 2008-May 2009.

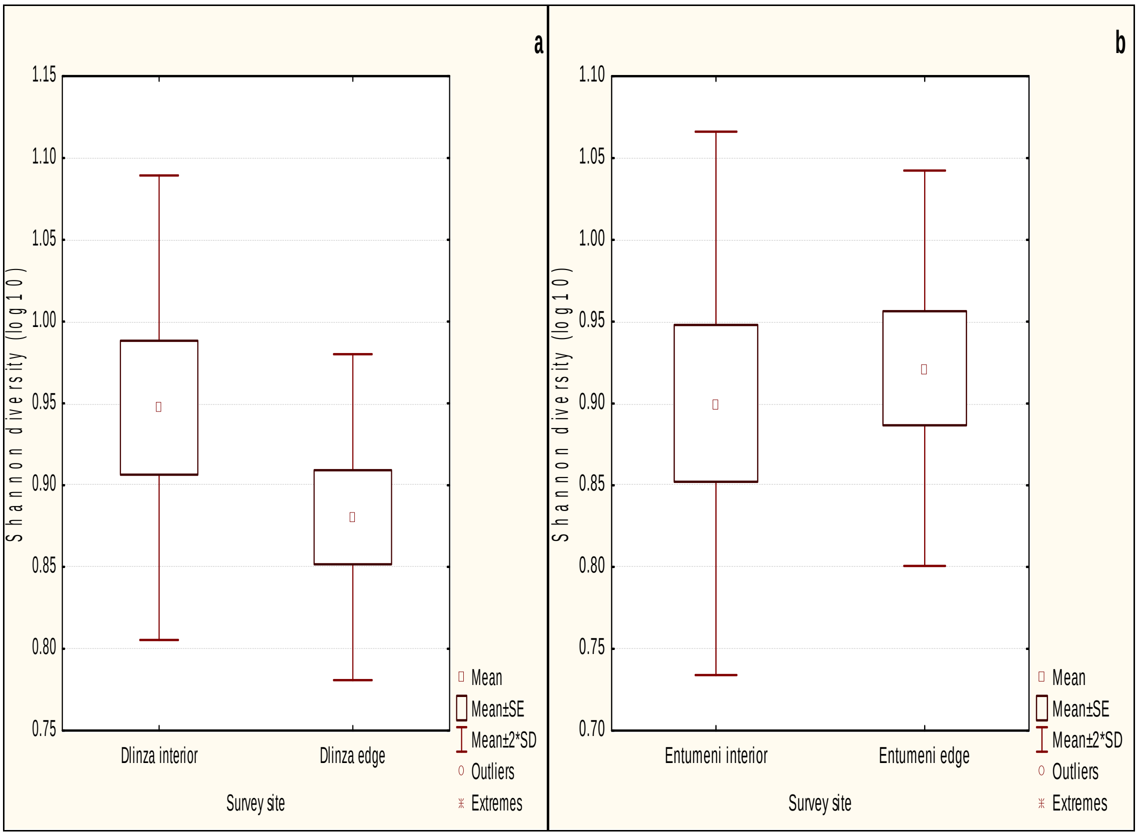


Fig. 27. Box and whisker plots showing the mean Shannon diversity (H') index of fruit-feeding butterfly assemblages recorded with baited traps at Dlinza (a) and Entumeni (b) forest interior and edge for the study period June 2008-May 2009.

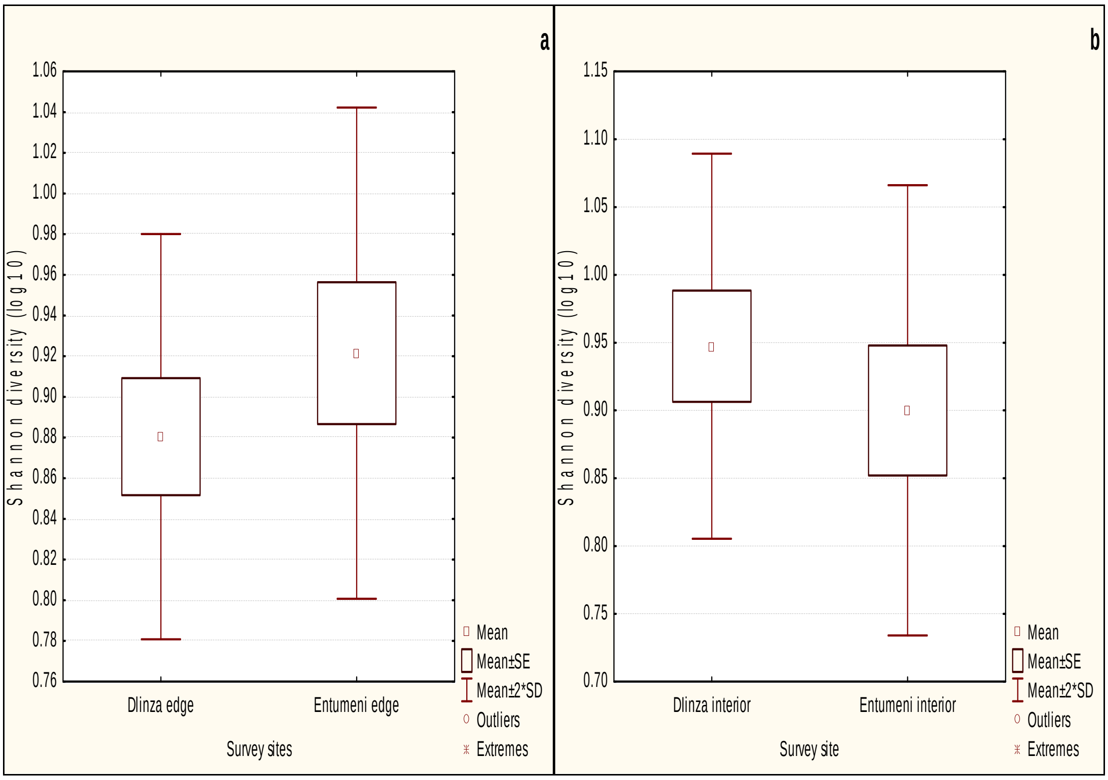


Fig. 28. Box and whisker plots showing the mean Shannon diversity (H') index of butterfly assemblages recorded with baited traps at Dlinza and Entumeni forest edge (a) and interior (b) for the first study period of June 2008 - May 2009.

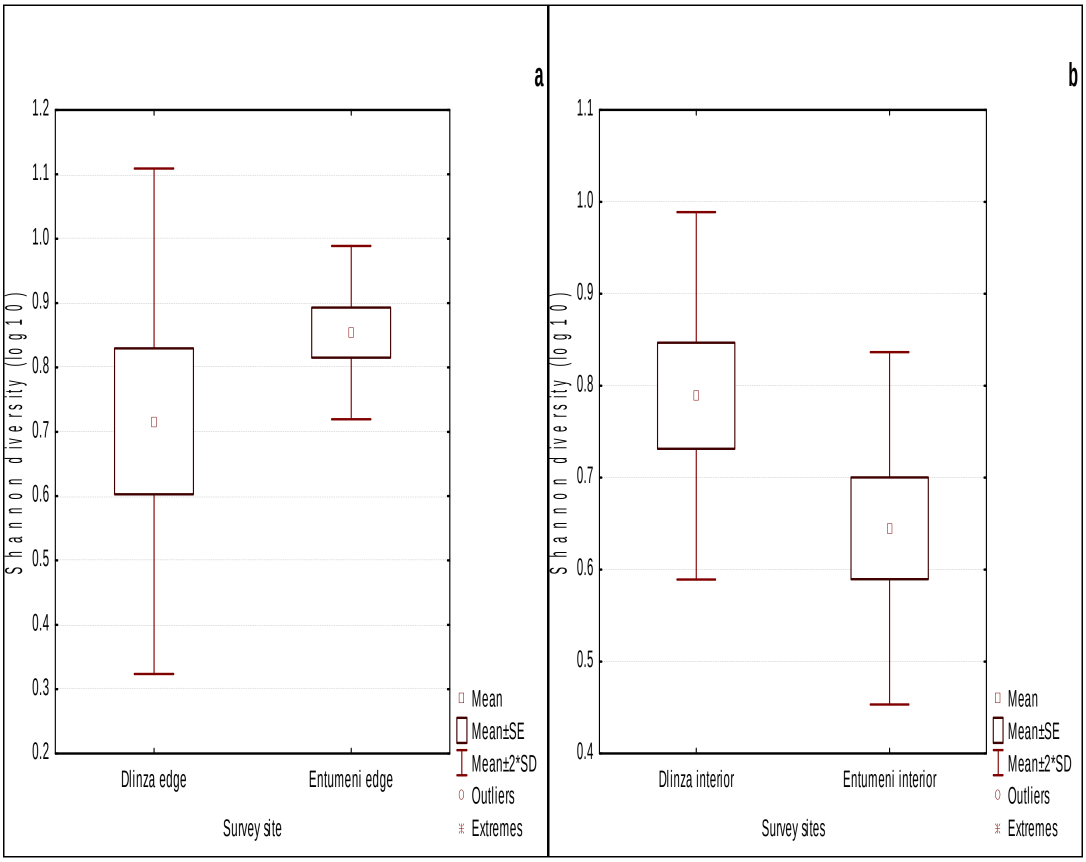


Fig. 29. Box and whisker plots showing the mean Shannon diversity (H') index of fruit-feeding butterfly assemblages recorded with baited traps at Dlinza and Entumeni forest edge (a) and interior (b) for the second study period March-May 2010 (autumn).

Diversity (Shannon index) at individual sites more often followed the average trends presented in the previous section. However, some results pertaining to individual sample sites are highlighted. Dlinza forest DI1 which was the only survey point located in the canopy had the highest Shannon diversity index in comparison to other survey sites in the forests for the period June 2008-May 2009 (Table 7). The survey site with the highest diversity index at Entumeni forest was EI3 during June 2008-May 2009 (Table 7). For the second study period March-May 2010, the highest diversity (Shannon index) was once again recorded at DI1 (viewing tower site). At Entumeni forest all three forest edge points had higher diversity indices (Shannon index) during June 2008-May 2009 in comparison to forest interior sample sites (Table 8).

4.3 Species composition of fruit-feeding butterfly assemblages

4.3.1 Similarity of species composition among forests and sample sites

A number of DCA ordinations were performed to analyse the relationship between the sample sites of Dlinza and Entumeni in terms of species composition (similarity in species and species abundances). Most of the DCA ordinations produce a crowded pattern of samples with a poor distinction of any groups along the x- and y-ordination axes. Two examples of such an ordination graphs are given in Fig. 30 and Fig. 31. In terms of total relative species composition of the interior sample sites and exterior sample sites at both forests, poor distinctions of any groups along the x- and y-ordination axes are also present.

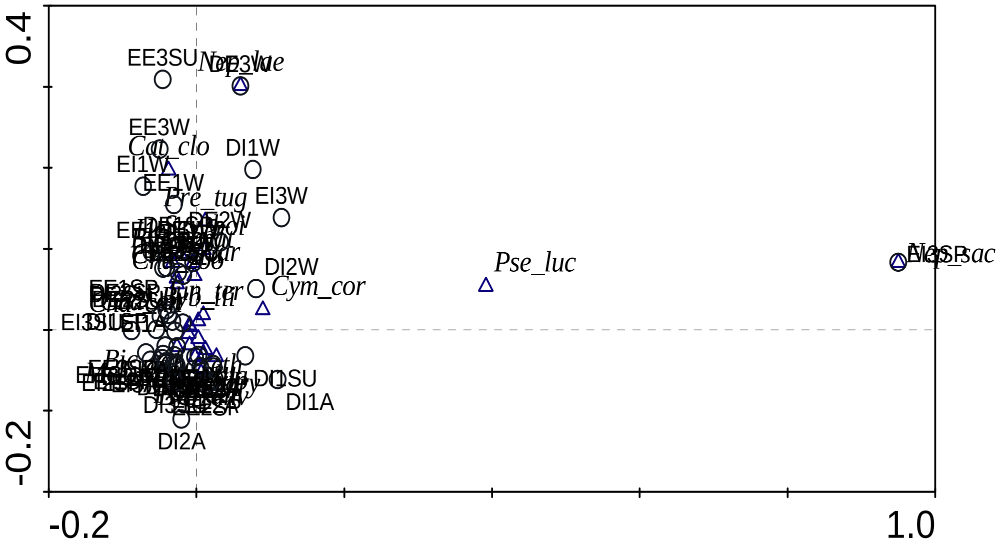


Fig. 30. DCA ordination graph of sample sites according to season of the year and species for butterfly assemblages recorded with baited traps at Dlinza and Entumeni forests during the study period June 2008-May 2009.

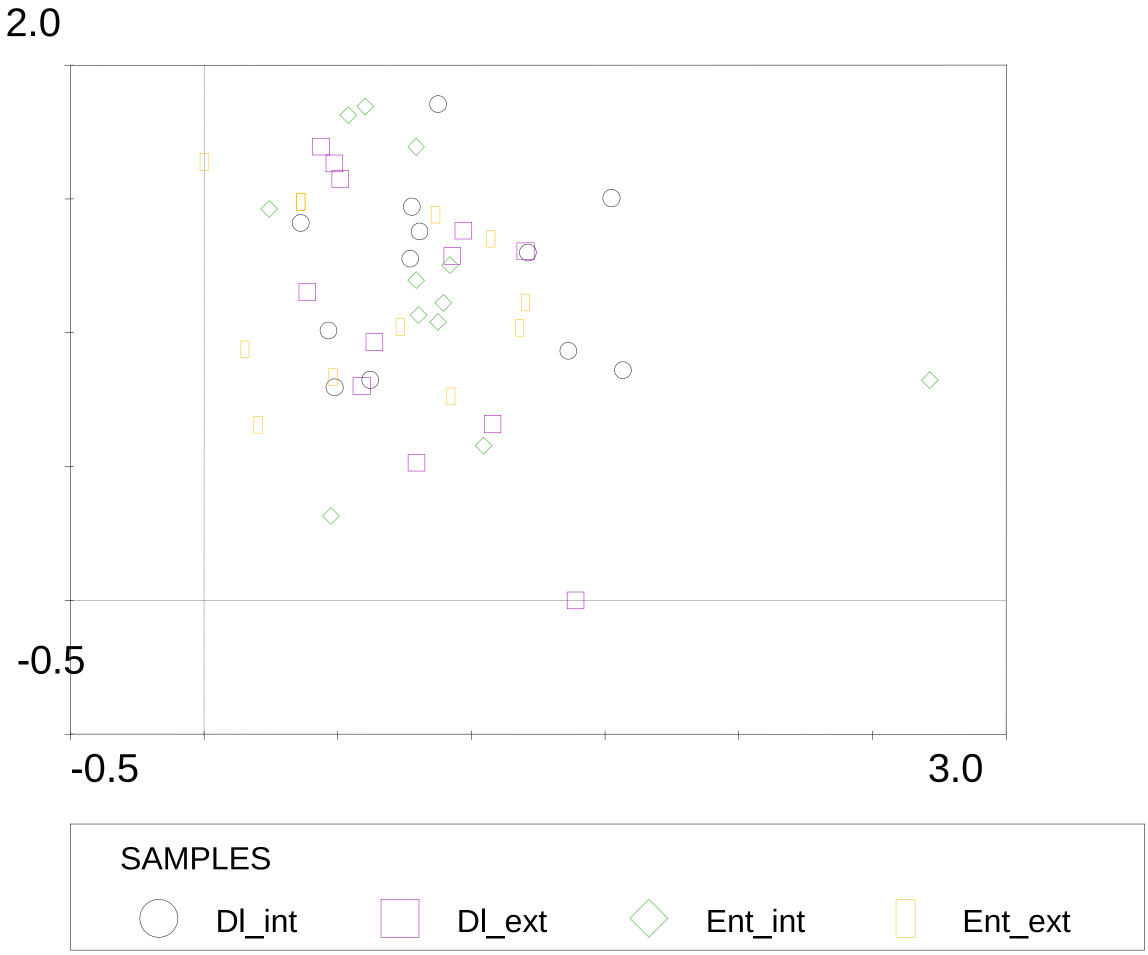


Fig. 31. DCA ordination graph of sample sites for butterfly assemblages recorded with baited traps at Dlinza and Entumeni forests for the first study period June 2008- May 2009.
Dl_int: Dlinza forest interior
Dl_ext: Dlinza forest edge
Ent_int: Entumeni forest interior
Ent_ext: Entumeni forest edge

DCA ordination graph of species shows four possible groupings (Fig. 32). On the left of the y- axis are a group of species which include *M. leda*, *B. anynana, C. cloanthe cloanthe, C. zoolina zoolina, H. perspicua.* A middle group consisting of *C. cithaeron cithaeron, C. candiope candiope, C. ethalion ethalion, B. safitza safitza, E. hiarbas angustata,* and *C. varanes varanes*. At the top of the graph there is a group consisting of *P. dendrophilus, C. xiphares peningtoni, C. jahlusa argynnides, C. brutus natalensis, and C. druceanus, druceanus*. On the right of the graph there are a group of species such as *N. laeta, N. saclava,* *P. lucretia, C. coranus coranus, S. natalensis, J. terea elgiva, J .tugela tugela* (Fig. 32). However, the groupings at both the x- and y-ordination axes are not well-defined.

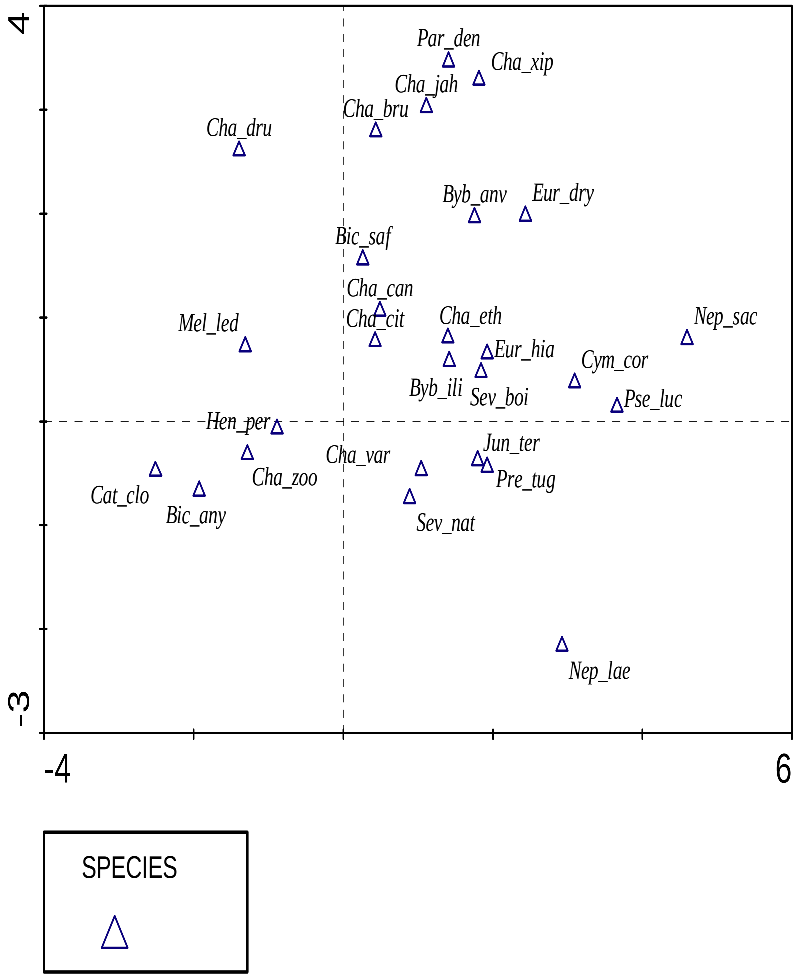


Fig. 32. DCA ordination graph of species of butterfly assemblages recorded with baited traps at Dlinza and Entumeni forests for the study period June 2008-May 2009.

4.3.2 Species responses

During the first study period 18 species were common to both forest reserves, of which 9 had higher densities at the larger Entumeni forest, 7 had higher abundances at the smaller urban Dlinza forest and 2 species had equal numbers at both forest patches (Table 3). Overall 7 species were trapped at Entumeni forest and not at the smaller Dlinza forest, while only 2 species were unique to Dlinza forest (Table 3). The species which were unique to Entumeni forest included, *M. leda, J. terea elgiva, B. anvatara, B. ilithyia, S. natalensis, N. saclava, and C. jahlusa,* while the two species which were only trapped at Dlinza forest were, *N. laeta and*

B. anynana. Of the nine *Charaxes* species trapped in the study area, 8 species were common to both forests with only *C. jahlusa argyinnes* unique to Entumeni forest (Table 3).

There was a significantly higher number of *C. cithaeron cithaeron* and *C. varanes varanes* trapped at the smaller urban Dlinza forest (p = 0.0016; p = 0.045) (Table 3). *C. candiope candiope* was also more abundant at Dlinza forest, while *C. ethalion ethalion* was clearly more abundant at Entumeni forest reserve (Table 3). The Satyrinae *B. safitza safitza* had a higher abundance at Dlinza forest.

When comparing the difference in species composition between the forest interior and forest edge at Dlinza forest, 17 butterfly species were trapped at both the forest interior and edge. There was only one species which was unique to the forest interior, *P. lucretia,* while the two species unique to the forest edge were *C. cloanthe* and *N. laeta* (Figs 33, 34). At Entumeni forest there were 12 species trapped at both the forest interior and edge. At this forest 3 species were unique to the forest interior, which included *M. leda, N. saclava,* and *P. lucretia* while the species common to the forest edge were *C. jahlusa, C. druceanus druceanus, S. natalensis, S. boisduvali, B. anvatara, B,ilithyia, C. cloanthe, J. tugela, J. terea elgiva,* and *H. perspicua perspicua* (Figs 35, 36). There were also differences in abundance of certain species between forest interior and edge. *C. candiope candiope* had higher numbers at both forest edges when compared to the forest interior (Figs 33-36).

B. safitza safitza was also more abundant at both forest edges when compared to the forest interior, with a greater variation at Dlinza forest edge (p = 0.011) (Figs 33-36). *E. dryope angulata* and *E. hiarbas angustata* had higher abundance at both forest edges when compared to the forest interior, with the variation greater at Dlinza forest (p = 0.0284) (Figs 33-36). Other butterfly species which were higher at the forest edge were *C. ethalion ethalion* and *C. varanes varanes* (Figs 33-36). The only butterfly which clearly showed the opposite trend of higher abundance at the forest interior in comparison to the forest edge was *C. coranus coranus* (Figs 33-36).

During the second study period, 3 species were unique to the larger Entumeni forest, while only one butterfly was unique to Dlinza forest (Table 4). 14 species were trapped at both forest patches, with 10 having higher numbers at Entumeni, 4 having higher abundances at Dlinza, forest, and 3 species having equal numbers at both forests (Table 4). Species only trapped at Entumeni forest were *C. cloanthe, B. anvatara, P. lucretia,* while *S. moranti* was the only butterfly trapped at Dlinza and not at Entumeni (Table 4). *C. cithaeron cithaeron* was again higher in abundance at Dlinza forest, however *C. varanes varanes* and *C. candiope candiope* were now marginally higher at Entumeni forest (Table 4). A higher number of *C. ethalion ethalion* were trapped at the larger Entumeni forest than at Dlinza forest. *E. hiarbas angustata* was a species which also had higher abundance at the larger rural Entumeni forest. *B.safitza safitza* however was higher at Entumeni during the second study (Table 4)

During the second study period of autumn 2010 there were 8 butterfly species common to Dlinza forest interior and edge. There were 4 species trapped only at the forest edge which were *C. ethalion ethalion, C. varanes varanes, C. zoolina zoolina,* and *E. dryope,* while the 3 species trapped only at the Dlinza forest interior were *C. coranus coranus, M. leda*, and *S. morantii.* At Entumeni forest 9 species were trapped at both forest interior and forest edge. There were 8 butterfly species unique to Entumeni forest edge with no species trapped only at the forest interior. Species attracted to the forest edge were *B. anvatara, C. cloanthe cloanthe, C. druceanus druceanus, C. zoolina zoolina, C. ethalion ethalion, E. dryope, P. lucretia* and *M. leda,*(Figs 33-36).

When comparing the species composition of individual survey sites, the lowest abundance of *B. safitza safitza* was at DI1 (Figs 37-40). DI1 also recorded the lowest abundance of *C. varanes varanes* within Dlinza forest reserve, with the most *C. varanes varanes* being trapped at DE1, however DI1 had the highest number of *Sevenia boisduvalli* and *Cymothoe coranus coranus* (Figs. 37-40). DI3 had the highest abundance of *C. cithaeron cithaeron* (Fig. 37.3)

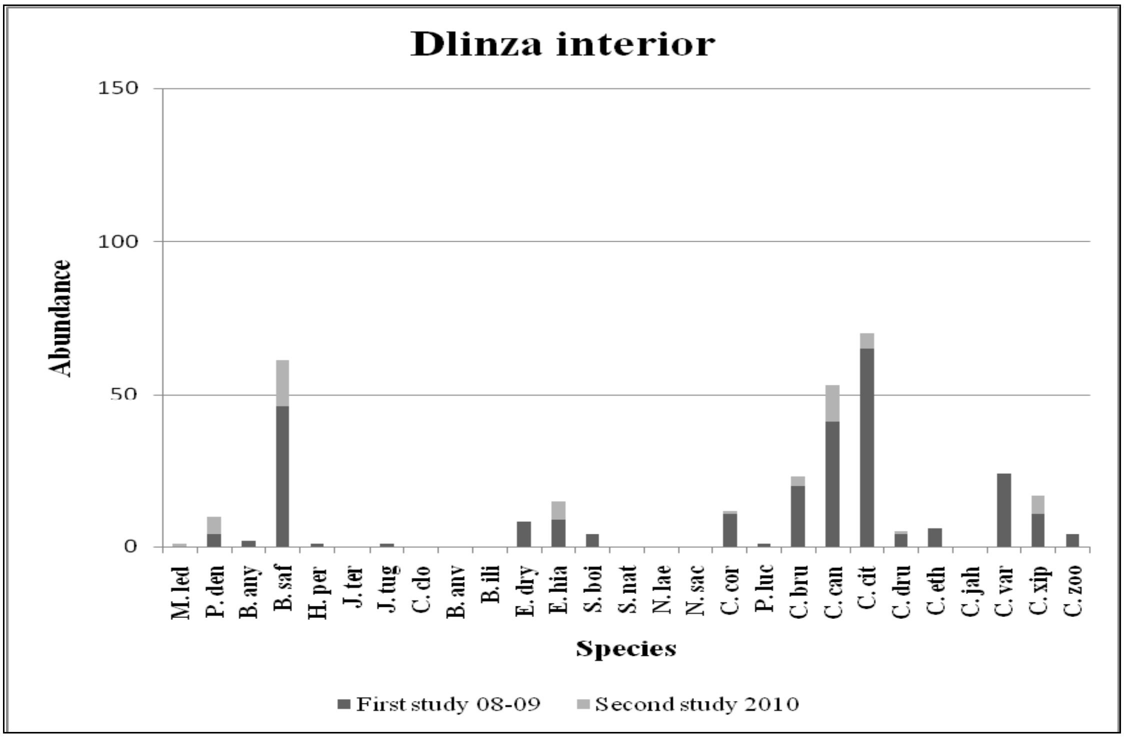


Fig. 33. Total abundances of fruit-feeding butterfly species recorded with baited traps at Dlinza forest interior for both study periods of June 2008-May 2009 and March-May 2010.

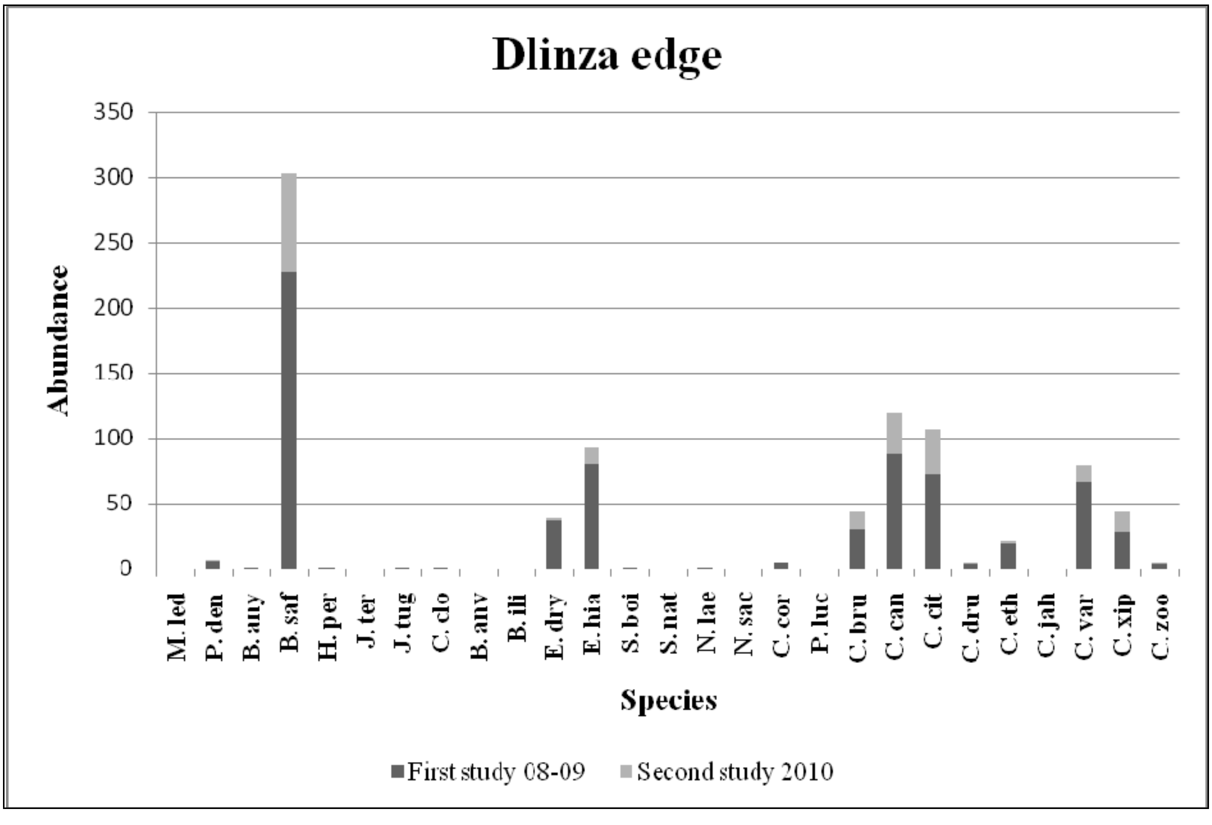


Fig. 34. Total abundances of fruit-feeding butterfly species recorded with baited traps at Dlinza forest edge for both study periods June 2008-May 2009 and March-May 2010.

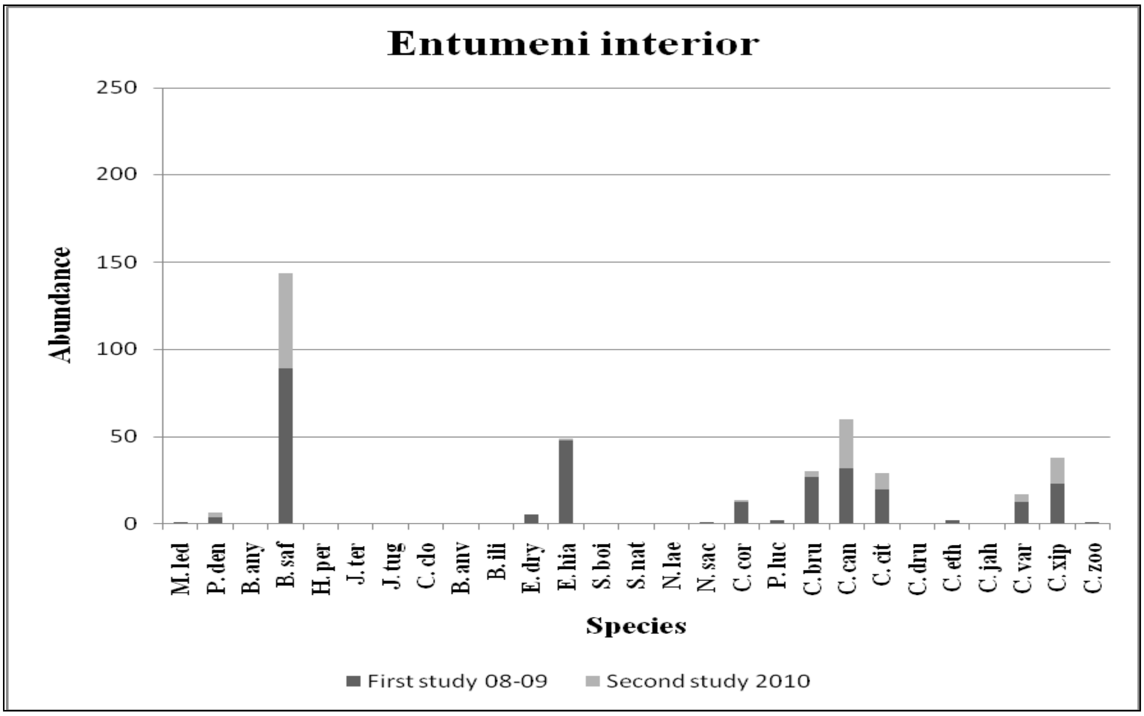


Fig. 35. Total abundances of fruit-feeding butterfly species recorded with baited traps at Entumeni forest interior for both study periods June 2008-May 2009 and March-May 2010.

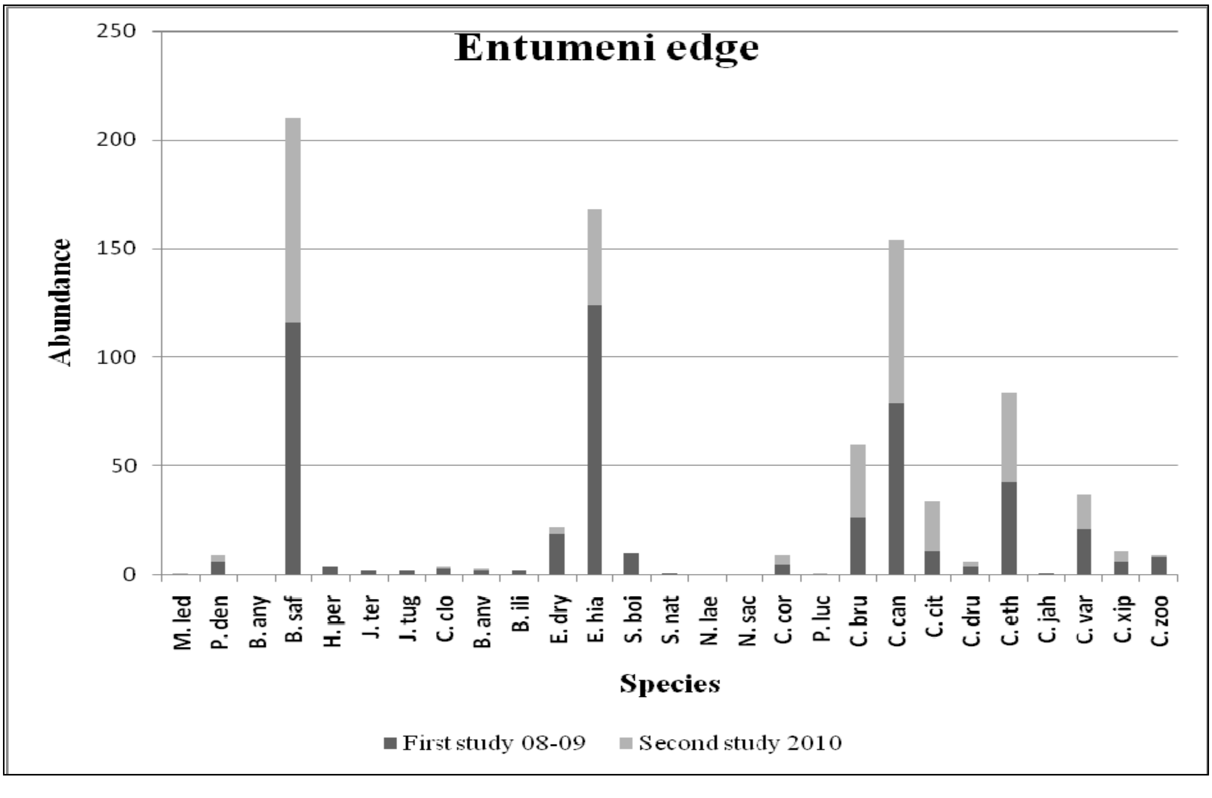


Fig. 36. Total abundances of fruit-feeding butterfly species recorded with baited traps at Entumeni forest edge for both study periods June 2008-May 2009 and March-May 2010.

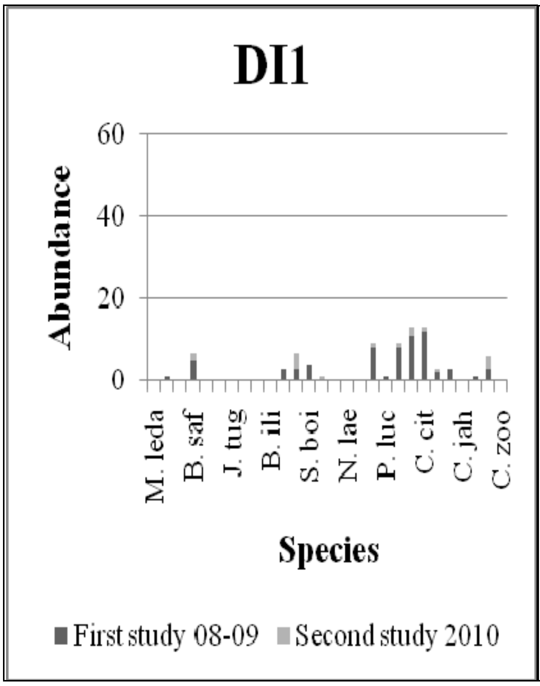


Fig. 37.1

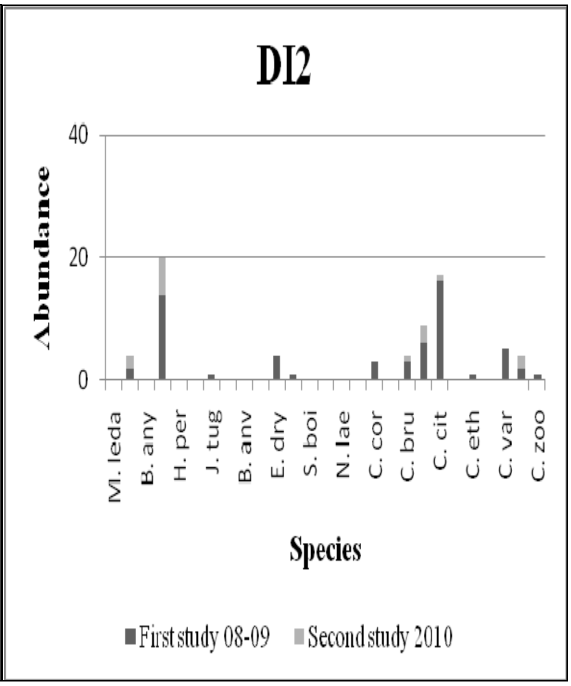


Fig. 37.2

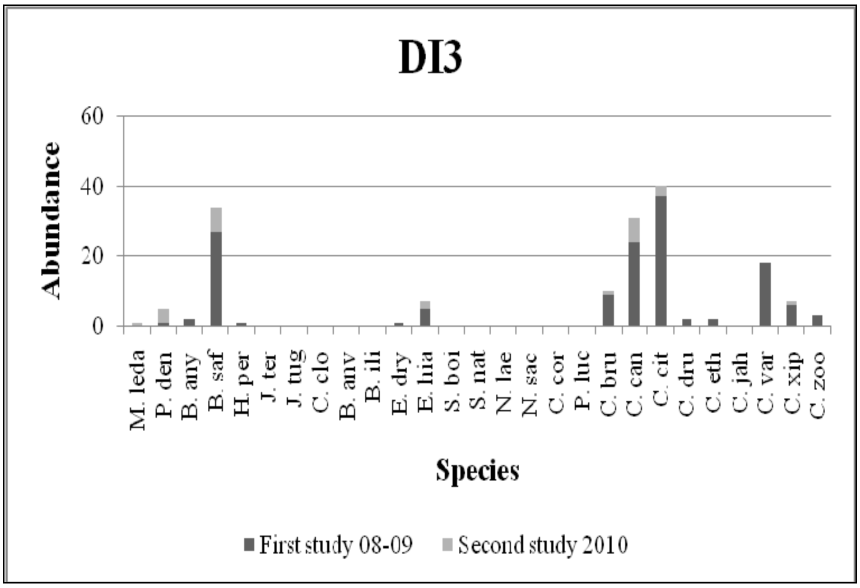
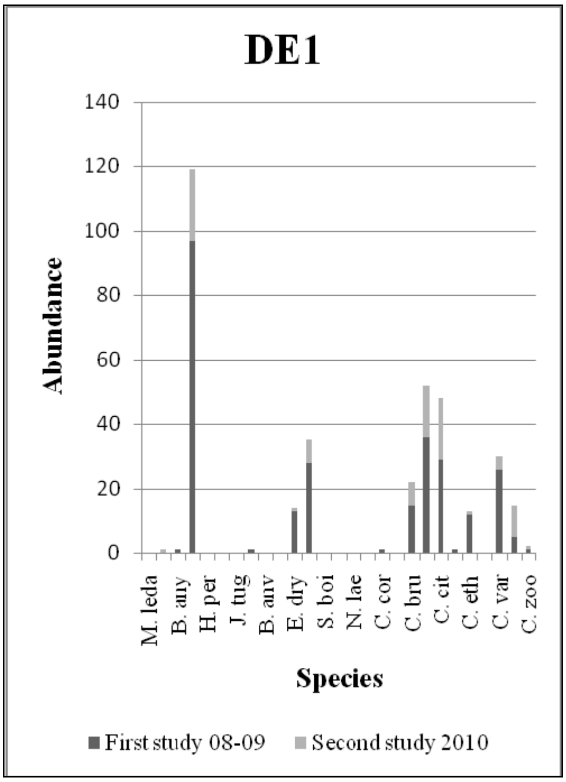


Fig 37.3

Fig. 37. Abundances of fruit-feeding butterfly species recorded with baited traps at Dlinza forest interior sample sites for both study periods June 2008-May 2009 and March-May 2010.



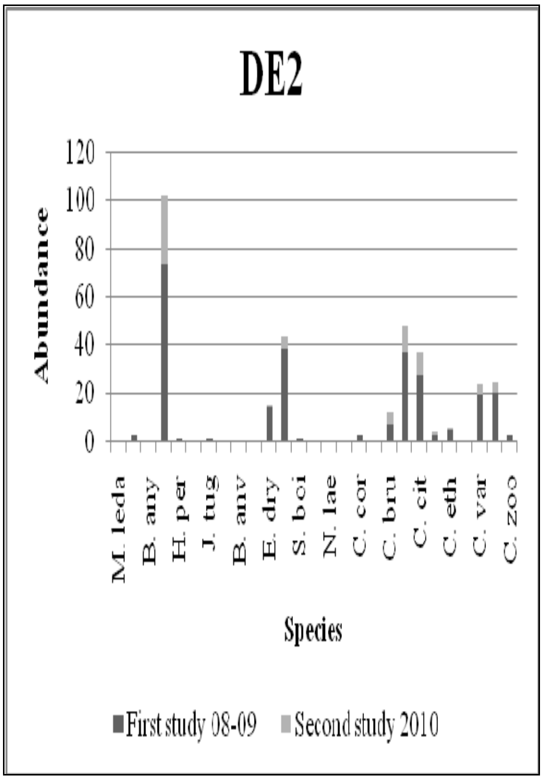


Fig. 38.1

Fig. 38.2

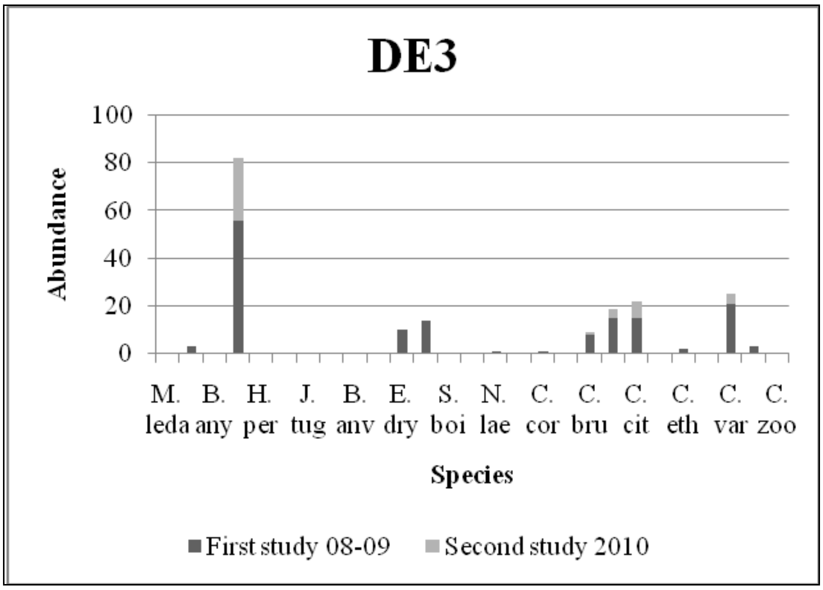


Fig. 38.3

Fig. 38. Abundances of fruit-feeding butterfly species recorded with baited traps at Dlinza forest edge sample sites for both study periods of June 2008-May 2009 and March-May 2010.

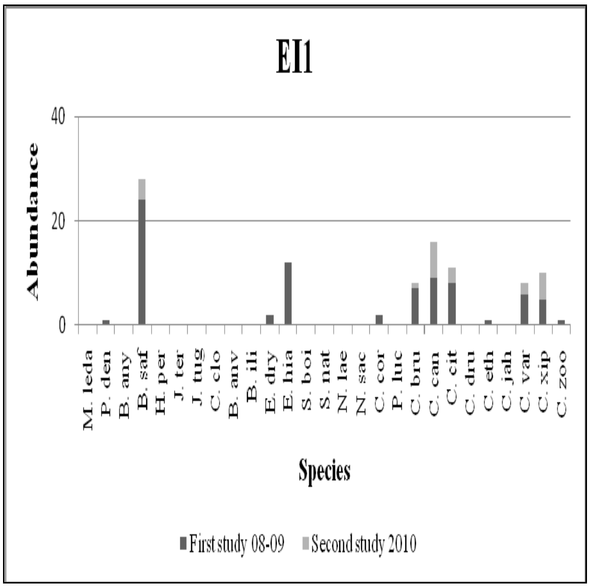


Fig. 39.1

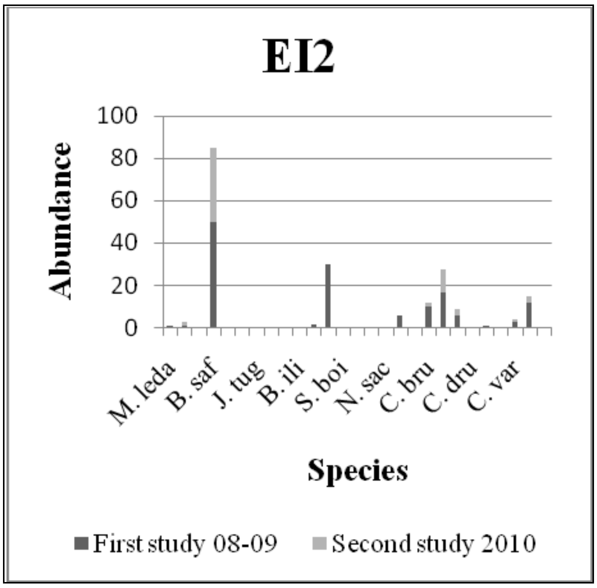


Fig. 39.2

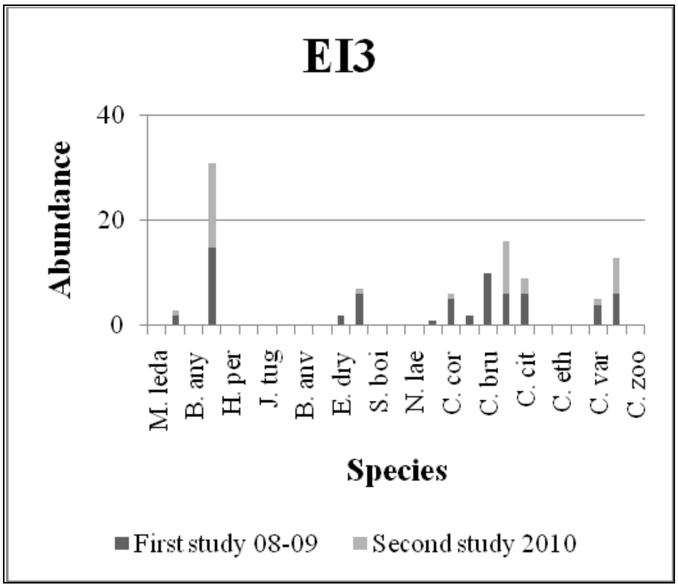


Fig. 39.3

Fig. 39. Abundances of fruit-feeding butterfly species recorded with baited traps at Entumeni forest interior sample sites for both study periods of June 2008-May 2009 and March-May 2010.

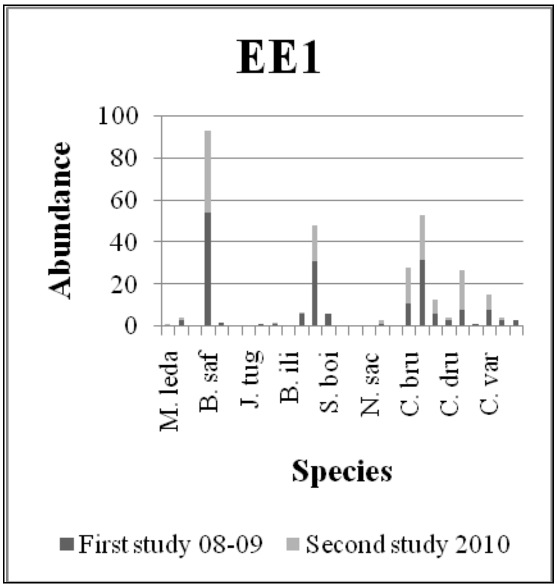


Fig. 40.1

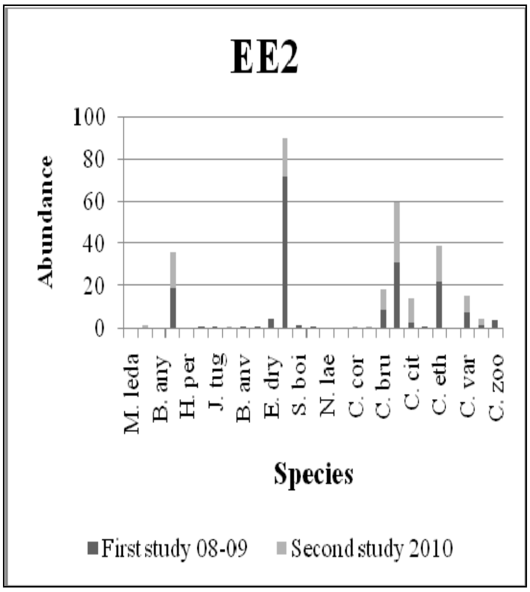


Fig. 40.2

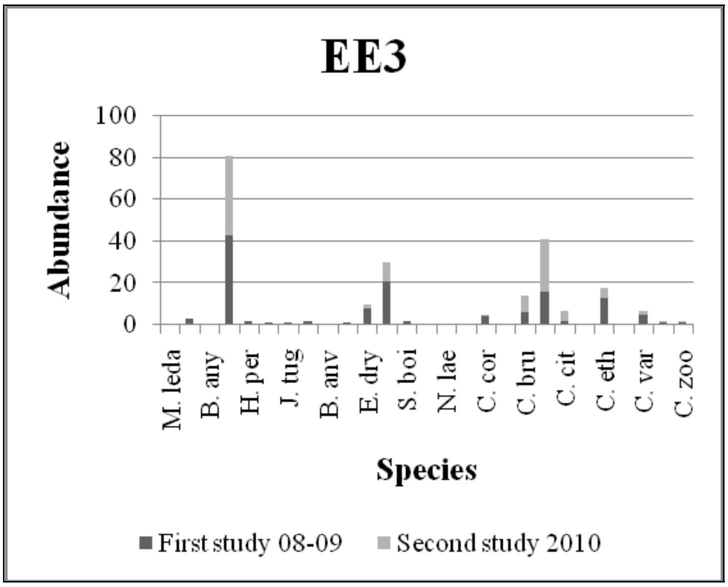


Fig. 40.3

Fig. 40. Abundances of fruit-feeding butterfly species recorded with baited traps at Entumeni forest edge sample sites for both study periods of June 2008-May 2009 and March-May 2010.

A number of seasonal responses of butterfly species are of interest. Autumn was the season when most butterfly species had the highest abundance. Most of the *Charaxes* species had the highest numbers in autumn, except for *C. druceanus druceanus, C. varanes varanes* and *C. zoolina zoolina* (Fig. 41). The flight period is also strongly seasonal for *C. xiphares penningtoni* with winter and spring being the season when this *Charaxes* species is mostly inactive. *C. brutus natalens is* mostly abundant during autumn with low abundance during spring (Fig. 41).

For the subfamily Satyrinae, there are also higher abundances recorded for *B. safitza safitza* and *P. dendrophilus* during autumn (Fig. 42). *P. dendrophilus* is mainly an autumn species and is not flying during the other seasons (Fig. 42). The low abundances observed for *M. leda, B. anynana* and *H. perspicua perspicua* are due to very few of these butterflies being trapped (Fig. 42).

Eurytela dryope angulata and *E. hiarbas angustata* were the dominant species trapped from the subfamily Biblidinae, with very low abundances from the other 3 species (Fig. 43). *E. hiarbas angustata* and *E. dryope angulata* also show the highest abundance in autumn, with *E. hiarbas angustata* having moderate abundance during winter (Fig. 43).

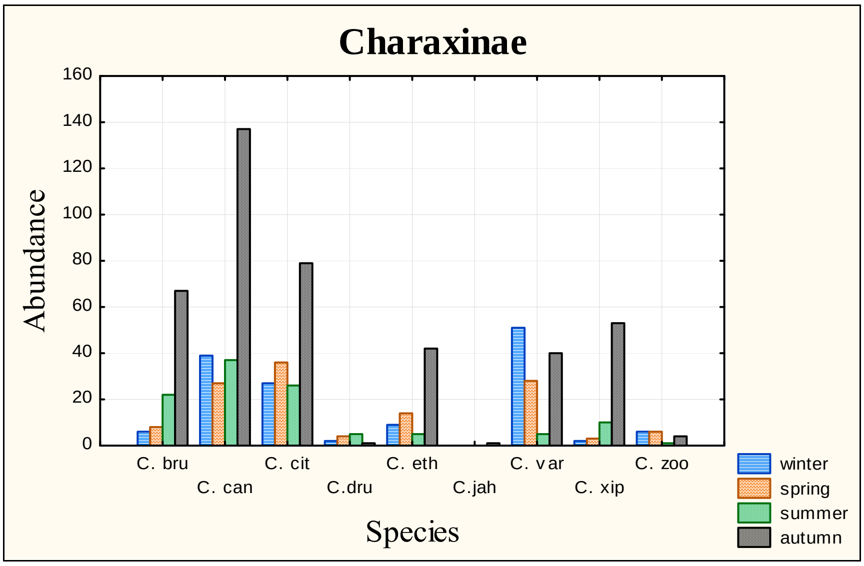


Fig. 41. Seasonal abundances of species belonging to the subfamily Charaxinae recorded with baited traps at Dlinza and Entumeni forests for the first study period June 2008- May 2009.

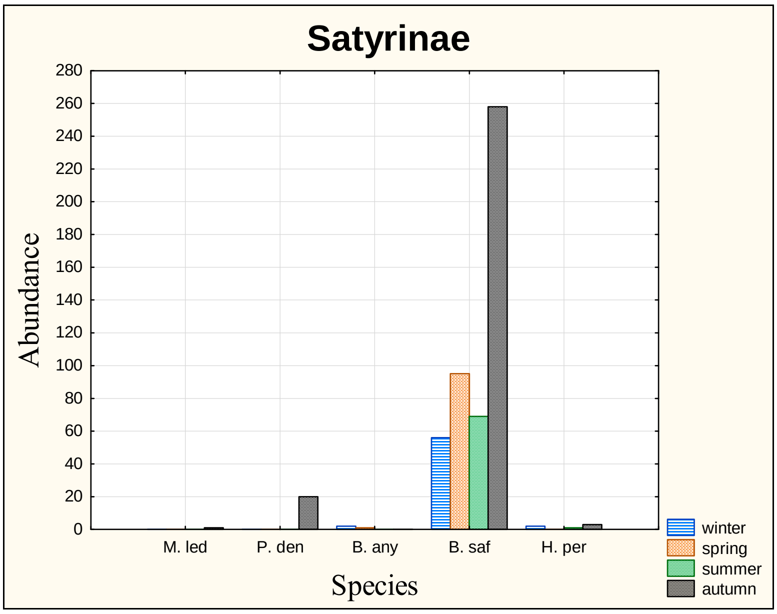


Fig. 42. Seasonal abundances of butterfly species belonging to the subfamily Satyrinae recorded with baited traps at Dlinza and Entumeni forests for the study period June 2008-May 2009.

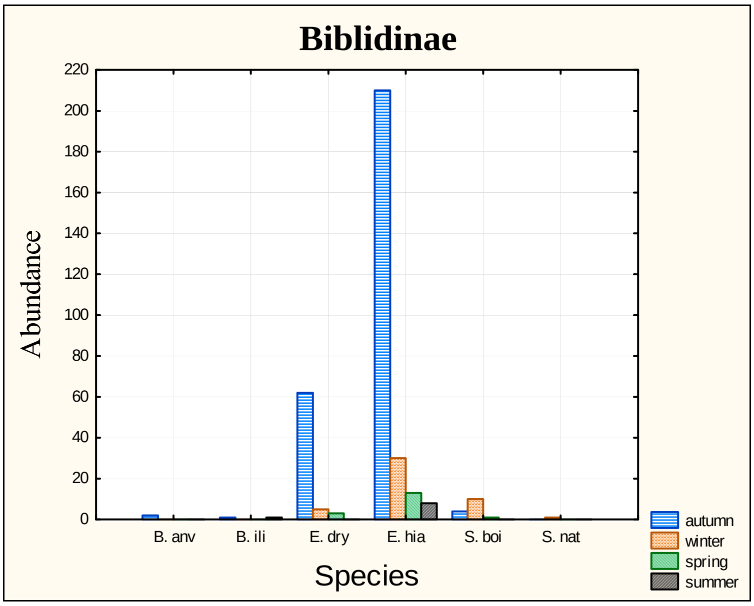


Fig. 43. Seasonal abundances of species belonging to the subfamily Biblidinae recorded with baited traps at Dlinza and Entumeni forests for the first study period June 2008-May 2009.

Fig. 44. *C. candiope candiope* and *C. ethalion ethalion* feeding on sap from a branch of *Albizia adianthifolia* at DI1 (viewing tower sample site) in Dlinza forest reserve. Photo: W.S. Forrester.

Fig. 45. *Paralethe. dendrophilus indosa* at forest pathway in Entumeni forest. Photo: W.S. Forrester.

CHAPTER 5: DISCUSSION

Such as highlighted in the introduction assemblage studies by nature entail numerous facets and many factors play a role in shaping the assemblage structure and species composition. This study is explorative and focused on emergent properties of the fruit-feeding butterfly assemblages recorded with baited traps at parts of the two forests, Dlinza and Entumeni. Discussion follows the hypotheses outlined in the introduction (Chapter 1). Hypotheses mainly focused on the suitability of baited traps for quantitative studies in non-equatorial forests, a mark-release-recapture technique, the influence of seasons on the assemblages, possible influence of altitude, forest size and possible effects of anthropogenic developments adjacent these forests. Besides addressing these hypotheses the study also describes fruit-feeding butterfly assemblage based on quantitative data and ultimately strives to make a contribution towards forest conservation from a unique angle, butterfly assemblages.

5.1 Suitability of baited traps for quantitative studies of fruit-feeding butterfly assemblages in South Africa

Hypothesis 1 in the introduction suggest that fruit-baited traps could be useful to study fruit-feeding butterfly assemblages in South Africa but could be limited by a relatively low number of species and abundances in a sub-tropical environment (if compared to tropical environments). Though exact numbers are not available enormous diversity of fruit-feeding butterfly species in tropical or equatorial Africa is conspicuous in literature, for example in Henning (1989), Kielland (1990), Larsen (1991; 2005), D'Abrera (1997; 2004). The overall butterfly abundance and species richness recorded at the Dlinza and Entumeni forests during this study was markedly lower than in other tropical countries of Africa and other areas of the world (Tables 3, 4). For example in Tanzania, Fitzherbert *et al.* (2006) captured 186 species over a period of 44 days, with 61 of these species being captured with baited traps. Uehara-Prado *et al.* (2007) trapped 1810 fruit-feeding butterflies consisting of 70 species over a 36000 hour study period in the Brazilian Atlantic forest. There are a small number of *Charaxes* species in the KwaZulu-Natal Province when compared to other tropical areas of Africa. According to Henning (1989) there are a total of 180 species of *Charaxes* in Africa with several new species described recently in the Afrotropical region, and 18 Charaxinae *species*-groups. Only 9 species were trapped in our study area, and 7 of these *species*-groups were found at Dlinza and Entumeni forests (Table 6). Despite this low number of *Charaxes* species the results show the value of small forest patches for the conservation of fruit-feeding butterfly species in the KwaZulu-Natal Province of South Africa (Tables 3, 4). Species accumulation curves show that sampling adequacy could be reached soon in these Kwa-Zulu Natal forests because the rate of species increase drop rapidly especially in autumn (Figs 10, 11).

According to O' Reagain (2001) there are approximately 85 species of butterfly that occur at Dlinza forest, therefore the 28 fruit-feeding species trapped at these two forest reserves contribute approximately 33 % of the total butterfly species reported to occur at these forest patches. This is a large percentage of the total butterfly fauna and shows the value of these fruit-feeding butterfly populations to the overall arthropod communities.

A similar study conducted in Kenya at two degraded forest remnants of 180 ha and 350 ha showed these forest patches to be important for butterfly preservation, and to contain viable populations of true forest butterflies (Rogo & Odulaja 2001). According to Ribeiro *et al.* (2008) most conservation efforts seek to preserve large pristine areas of continuous forest. However this study clearly indicates the importance of preserving local fragmented landscapes, even small urban reserves such as Dlinza forest, which are extremely valuable for the preservation of fruit-feeding butterfly species.

Owing to the overall trapping of 2801 individuals and 28 species, if all the efforts in a year cycle and an additional autumn survey are counted, at these two forest reserves it is clear that this survey technique is useful in studying fruit-feeding butterfly assemblages in forests of KwaZulu-Natal, and should be included in any future surveys or conservation planning of forest butterflies in South Africa. Results supports hypothesis 1 that baited traps could be used in quantitative studies of South African forests and the number of species and abundances obtained exceeded expectations.

In other regions of the world studies using bait traps have also resulted in useful conclusions, and showed the fruit-feeding butterfly group to be a valuable indicator of forest disturbance in Brazil (Barlow *et al.* 2007; Uehara-Prado *et al.* 2007), to be positively correlated with habitat area in Borneo (Benedick *et al.* 2006), and to be unaffected by selective logging three years later in Belize (Lewis 2000). The design of the bait traps in these other studies may however have differed in comparison to the bait trap design in the present study. The bait trap used in our study were cylindrical tubes and was without any internal funnel as those stated in the Uehara-Prado *et al.* (2007) study in the Brazilian Atlantic forest (Fig. 8). The design of the bait-trap in this study could account for the occasional escape of butterflies, however bait traps were long cylindrical tubes which measured approximately 1.02 m in length, compared to a similar study in Brazil which used bait traps which were shorter at 0.90 m and were reported to minimize butterflies escaping (Barlow *et al.* 2007). It is essential to use bait traps for sampling the fruit-feeding butterfly guild. According to Larsen (1991) any attempt at sampling forest butterflies demands the use of traps or more than half the Charaxinae and some of the genus *Bicyclus* species will be missed.

This technique should however be explored further in future studies with regard to certain aspects. For example, are there limitations of sampling with baited traps only from the under-storey of the forest. There have been reports that vertical stratification of forest butterflies may not give an accurate account of fruit-feeding butterfly assemblages in a forest when using these traps only in the under-storey (Uehara-Prado *et al.* 2007). Walla *et al.* (2004) found vertical structure among fruit-feeding butterflies varies with geographic location and that considerable seasonal variation in species abundance was found between under-story and canopy samples. Another study conducted by De Vries *et al.* (1997) in an Ecuadorian rainforest found butterfly species richness of the fruit-feeding guild were unequally distributed between forest canopy and under-storey with 19 % of species only in the canopy, 34 % in the under-storey, and 47 % shared between the two strata. Therefore for valid comparisons to be made, studies should sample from all vertical strata in tropical forests (Pin Koh 2007). Although it is possible to hoist bait traps into the canopy there are logistical constraints involved if many traps are to be used. In the present study the smaller urban Dlinza forest had an aerial boardwalk and viewing tower in the forest which made it possible to have DI1 positioned in the canopy twenty meters above the forest floor.

DI1 which was the only survey point located in the canopy in the present study had a higher species richness (d) and Shannon diversity index (H’) than the other five survey sites in Dlinza forest during both study periods (Tables 7, 8). Although diversity indices can be very misleading in conservation evaluation (Akite 2008), this observation may be an indication that there is variation in fruit-feeding butterfly assemblage structure between canopy and under-storey at Dlinza forest. At Entumeni forest there was no viewing tower and all survey sites were located in the under-storey making a comparison between under-storey and canopy impossible. Further surveys should be conducted where sampling is done at both canopy and under-storey level to draw clearer conclusions in this regard. However looking at the results in the present paper, I am confident that the data gives a good indication of overall assemblage composition between survey sites.

Another aspect which could affect data collection with bait traps is the timing of the deployment of the traps. In the present study bait traps were taken down and re-deployed at each sampling occasion giving a maximum of five hours of effective capture time per day, while several other studies bait traps were left in position for the duration of the entire study period with an effective capture time of ten hours a day, with fresh bait added after a certain time period had elapsed (Benedick *et al.* 2006; Uehara-Prado *et al.* 2007). The reason traps were not left in position during the present study was that more than one forest was sampled with the same traps, and bait-traps may have been stolen. During a study in Tanzania bait traps were stolen at night and had to be removed and taken back to camp at the end of the day (Kielland 1992).

Leaving the traps in position for the entire study could possibly affect the results, as certain butterfly species such as the Satyrine *M. leda helena* are reported in the literature to be more active at dusk (Kemp 2002; Woodhall 2005), therefore if traps are emptied at 14.00 hrs as they were in the present study the abundance of *M. leda helena* may be lower than if traps were left in position and not taken down at the end of the day as they were in several other studies.

The spatial positioning of the bait traps can also vary according to the study. During certain studies bait traps were disposed linearly along pre-existing trails, suspended 1.8-2.2 m above the ground with a distance of at least 20 m between adjacent traps (Uehara-Prado *et al.* 2007), while in Borneo 20 bait traps were hung at 100 m intervals along 2 km of transects at each site (Benedick *et al.* 2006). In the present study a single trap was positioned at each survey point, with three bait traps at the interior of the forest and three traps at the forest edge. These bait trap locations were selected randomly where forest openings occurred with the distance between traps being ≥200 m.

Other possible limitations with this survey technique are that butterflies do escape from the baited traps, however this is thought to have had no significant effect on the actual results. According to Larsen *et al*. (2009) the Genus *Cymothoe* are reluctant to enter bait-traps, and species such as *Catuna* and *Euriphene* readily escape baited traps after feeding owing to their ground-hugging flight. During the present study *C. coranus coranus* did enter the bait-traps however they appeared to exit the traps more frequently than other butterfly species.

With regard to disturbance of the traps, although the primate group *Chlorocebus pygerythrus* are abundant in certain areas, low numbers were observed in these forest patches and therefore no disturbance was noted. Even excessive wind did not have a negative effect on sampling as the bait in the traps was secured by placing the bait in a plastic container which fits into a hole cut into the board suspended below the bottom of the trap (Fig. 9). The bait is therefore not easily overturned. Moderate or even fairly strong wind appears to have little effect on butterflies coming into the bait-trap, as high captures were recorded on windy days. A further limitation could possibly be that when natural fruit is available in the forests, bait traps could become less attractive to butterflies (Barlow *et al.* 2007).

The advantages of this technique are that although this data collection method only samples certain species from the family Nymphalidae, this method allows for accurate species identification which may be a limitation with other data collection methods such as transect, and point surveys (Lewis 2000). Similar bait traps used during a study in Tanzania returned the same overall pattern of species richness across habitats as sweep nets (Fitzherbert *et al.* 2006). It also allows for sampling in several areas simultaneously with a relatively similar sampling effort (Ribeiro *et al.* 2008), and can also be used effectively for Mark-Release-Recapture studies. Large numbers of butterflies can be marked within a relatively short time period, and with minimal effort. Approximately 190 individuals were trapped in one bait-trap during a five hour period in the present study.

5.2 Mark-release-recapture of fruit-feeding butterflies in the Dlinza and Entumeni forests

According to hypothesis 2 a mark-release-recapture technique will show a moderate turnover of species which may imply moderate abundances of species, with a lesser turnover at the smaller Dlinza forest.

Very low numbers of recaptures recorded in the present study supports hypothesis 2, and would indicate the populations of fruit-feeding butterflies at these two forest patches are large and that there is a high turnover of species (Table 2). The lack of dispersal between forest patches is noted, and this could be problematic for conservation issues such as maintaining metapopulation structures for the populations and ultimately the assemblage. According to Brereton (2004) in a fragmented environment maintaining viable population networks (metapopulations) is crucial to butterfly survival, and evidence is accumulating that extinction may be a regular feature of the dynamics of many butterfly populations (Erhlich 1989; Boggs *et al.* 2000). However, isolation of habitats may not have a negative effect on butterfly species richness (Krauss *et al.* 2003). From the low number of recaptures recorded at both forests in this study it is clear that these forests are capable of supporting viable populations of fruit-feeding butterfly species. A number of reasons could be given for this lack of dispersal between patches. For example, the approximately 7 km distance between Dlinza and Entumeni may be too far for these fruit-feeding butterflies to disperse. According to Larsen (1991) the majority of Afrotropical butterflies depend on forests for their survival and are reluctant to cross inhospitable terrain, although some species have colonizing powers. For some species, even narrow bands of unsuitable habitat may act as effective barriers to movement (Natuhara *et al.* 1999), with limited dispersal in smaller populations being associated with increased extinction risk (Schultz & Cronje 2004) due to lower genetic diversity (Vandewoestijne & Baguette 2004).

However several mark-release-recapture studies have found extensive dispersal events. For example, Auckland, Debinski & Clark (2004) found a marked male *P. clodius* 12 km outside their study area. Néve *et al.* (1996) also found the butterfly species *P. eunomia* may move across several kilometers of unfavourable habitat, however they suggest these movements are exceptional, and that dispersal distances of 10 km may be too great for recolonization of unoccupied habitats.

Butterflies belonging to the subfamily Charaxinae are strong fliers (Henning 1989), and *C. varanes varanes* and *C. brutus natalensis* have been observed flying across sugarcane fields far from suitable forest habitat. These anecdotal observations have been made on several occasions by the author. Therefore distance appears to be unlikely as an explanation for lack of dispersal between forest patches. Another explanation could be that these butterflies avoid dispersal, as movement between patches exposes them to dessication and predation

(Humpden & Nathan 2010). Another reason could be the forest edge prevents or reduces the chance of dispersal events. Auckland *et al.* (2004) suggest habitat edges probably have a greater effect on limiting dispersal than distance, especially strong edges such as those between grassland and forest. Studies have shown generally that individuals tend to avoid crossing into very different habitat types (Ries & Debinski 2001). This theory would be consistent with this study area as Dlinza and Entumeni forests are embedded in grasslands, and have distinct habitat edges (Fig. 5). There are however small pockets of forest between Dlinza and Entumeni which could act as stepping stones (Fig 2). Dispersal could therefore be taking place for this subfamily especially where there are these dispersal corridors. This emphasizes the importance of dispersal corridors or stepping stones between forest fragments (Néve *et al.* 1996). Rogo & Odulaja (2001) found high species similarity between two forest remnants in Kenya and suggest if dispersal corridors were established gene flow would be possible which would reduce local extinction.

It is unknown why no *B. safitza safitza* were recaptured in the present study as high numbers of this butterfly species were marked. It is possible that the marking of this Satyrinae species caused higher mortality as it is not as robust as the larger *Charaxes* species. It could also mean that the *Charaxes* species is more sedentary and that the *Bicyclus* species moves away from the area where it was marked.

Future research opportunities could be to conduct additional Mark-Release-Recapture (MRR) studies in the area and possibly include sampling at the smaller indigenous forest pockets between these larger remnants to establish whether there is dispersal between these forest patches.

5.3 Influence of seasonal changes on assemblage structure and species composition

Hypothesis 3 of this study states that seasons are expected to influence species abundance and species richness and an optimal time for fruit-bait surveys will be in late summer or autumn. A high abundance and species richness were recorded during autumn (March-May) and winter (June-August) and this has significant implications for any future assessment or study of these fruit-feeding butterfly assemblages (Figs 14, 15). These months should not be excluded from any environmental surveys or conservation planning of forest butterflies in KwaZulu-Natal.

Other studies also found seasons to be the most important abiotic factor affecting community composition of forest Lepidoptera (Summerville & Crist 2003; Barlow *et al.* 2007). Significant changes in butterfly species diversity between the dry and wet season have also been found in other studies (Humpden & Nathan 2010). The observation that butterfly abundance and species richness differs between seasons, and that autumn is an optimal time for sampling forest butterflies supports our hypothesis 3, however winter was higher in abundance and species richness rather than late summer as predicted. Higher abundance and species richness observed in winter and autumn could be as a result of many factors. According to Woodhall (2005), which is in general a field guide based on the experience of South African lepidopterists, many of the *Charaxes* species are more abundant during autumn. Therefore the higher abundance recorded during autumn in the present study would agree with the South African butterfly literature and experience of Lepidopterists. The timing of fruit set in these forests could partially explain this higher abundance and species richness. Horner-Devine *et al.* (2003) found fruit development peaked in the dry season, and suggest that forest butterflies may concentrate their distribution in or near the forest during the dry season. The subtropical climate in this study area with low variation in temperatures between summer and winter, being not far from the coast, could partially explain this observation and it is believed that in higher altitude temperate climates greater variation in abundance and species richness between summer and winter would be found.

The reason for the seasonal differences in butterfly abundance between forests, and between forest edge and forest interior within patches is complex, and at this stage is unclear as this study was mainly of an explorative nature. However many factors have been recommended by other authors as contributing to differences in assemblage structure between seasons, such as resource availability and light conditions (Ide 2000), rainfall (Henning 1989; Barlow *et al.* 2007), leaf quality (Murakami *et al.* 2008), temperature (White & Kerr 2007), and the number of plant species in flower (Ramírez 2006). According to Henning (1989) the *Charaxes* butterflies fly throughout the year over most of their range in Africa with peaks at certain times, usually after the rains.

As the adults of fruit-feeding butterflies are not nectar-feeding and therefore do not depend on flowers for their resources, their larvae are phytophagous and therefore should be positively related to the onset of new growth in their associated larval host plants. According to Murakami *et al.* (2008) leaf quality has a strong effect on the structure of lepidopteran larval communities, and young spring leaves with high nitrogen content were an important factor affecting larval communities. The overall higher abundance at Entumeni forest during winter could be as a result of resource availability (Fig.16). Entumeni is a larger forest and would have a greater number of larval host plants, which could mean higher numbers of butterflies emerging during this season. Due to the subtropical climate of the region many tree species may have new growth in autumn and winter which could result in a higher abundance at this larger forest patch in winter. The overall higher abundance at Dlinza forest during spring and summer when compared to Entumeni forest could be a result of higher rainfall at Dlinza forest during the wet season which could result in higher resources (Fig. 16). Although rainfall was not measured during this study, it appears from weather data that the rainfall is consistently higher at the lower altitude Dlinza forest.

The overall higher number of species trapped at Entumeni forest for winter, summer, and autumn was expected and could be due to the greater variation in topography with the associated higher habitat diversity which leads to a greater range in microclimates (Fig. 17). Vegetation structure is correlated with microhabitat characteristics like temperature, humidity, and luminosity (Ribeiro *et al.* (2008). The equal number of butterflies trapped at the forests during spring could be as a result of the higher rainfall at the lower altitude Dlinza forest during the rainy season which resulted in higher resource availability (Fig. 17)

The higher abundance at Entumeni forest edge during winter, spring, and autumn in comparison to the forest interior could be partly explained by microclimates (Fig. 18). According to Ide (2000) the Satyrine *Lethe diana* dispersed between forest edge and forest interior in response to temperatures and resource availability and was more frequent at the forest edge during cooler weather. Temperature has been found to affect butterfly species richness to a greater extent than habitat heterogeneity at fine spatial scales and is generally more important than precipitation (White & Kerr 2007). At Dlinza forest the trend was a higher abundance at the forest edge during all seasons (Fig. 18). This difference observed between the two forests could be partly explained by a change in microclimates at Dlinza forest edge due to the urban development and paved roadways surrounding this forest reserve, which could alter the microclimate at Dlinza forest edge in comparison to Entumeni edge. In contrast to Entumeni forest edge, all of the edge survey sites at Dlinza forest have paved roadways and residential areas in close proximity to the bait-trap locations. Further research opportunities could be to undertake studies at these two forest remnants where several abiotic variables such as temperature and humidity are compared between the forest interior and edge. A study undertaken in the Brazilian Atlantic forest on fruit-feeding butterflies showed microhabitat changes are exacerbated by constant anthropogenic pressures such as wood extraction, and hunting (Ribeiro *et al.* 2008).

It is clear from this study that the assemblage structure in terms of abundance, species richness and diversity differ significantly in seasons. A follow up study in autumn 2010 confirmed the high abundance, species richness and diversity in autumn at Dlinza and Entumeni forests. Winter was also productive in terms of abundance, species richness and diversity of fruit-feeding butterfly assemblages. Viable winter surveys to assess aspects of forest biodiversity could be valuable when many other assessments could be less effective. Species composition also changes, with the addition of species such as the relatively large satyrine *Parelethe dendrophilus indosa*. Reasons for these seasonal responses of butterfly assemblages appear to be more complex than a mere build-up in biomass and deserve more research.

5.4 Comparison of fruit-feeding butterfly assemblages recorded in forest interiors (clearings) versus forest edges

Assemblage (community) structure of organisms entails the abundances, species richness and diversity of assemblages. Differences between these components of assemblages relates to three hypotheses that have been presented in the introduction (Chapter 1) of which the first one is hypothesis 4. Hypothesis 4 states that forest edge assemblages at both reserves have higher species richness and diversity on average compared to species richness and diversity from forest interior survey points.

Within forest patches the significantly higher abundance recorded at Dlinza forest edge in comparison to the forest interior would be due to an edge effect suggested by Uehara-Prado *et al.* (2007), where certain butterfly species utilize host plant species such as Euphorbiaceae which are more abundant at the edge of smaller fragmented forests (Fig. 19a). The host plant of the Charaxinae butterflies is mainly from the family Fabaceae (Henning 1989). Several other studies have also found higher butterfly densities at the forest edge (De Vries *et al.* 1997; Vu 2008). A reason for these higher abundances at the forest edge are because forest edges are located between the forests and open land where both forest species and open species are present which results in higher numbers of species and individuals (Vu 2008). This higher abundance may also indicate higher disturbance. Disturbed forests have gaps and openings that attract more species and individuals (Vu 2008). In Borneo the abundance of Liana specialists were also found to be higher in road sites and where the forest edge is most prominent (Cleary *et al.* 2005). However the reaction to disturbance can be species specific as the densities of another forest species *S. parhassus* was not found to be correlated with the degree of habitat disturbance, and this was thought to be owing to the fact that this butterfly was taking advantage of increased light levels as a by-product of forest disturbance (Bonte & Van Dyck 2009).

The higher abundance at Entumeni forest edge in comparison to the forest interior although not significant, could partly be explained by the high habitat diversity adjacent to the forest edge (Fig. 19b). This higher habitat diversity resulted in the trapping of higher numbers of *E. hiarbas angustata* as well as other low density and rarer species such as *J. terea elgiva, B. anvatara, B. ilithyia,* and *C. cloanthe cloanthe,* of which the latter is predominantly a grassland species (Table 3). Former grasslands are mostly absent from the smaller Dlinza forest reserve, and have been replaced by various forms of land-use such as residential housing, sports fields, and paved roads.

Higher abundances observed at both forest edges in comparison to the forest interior could also be partially explained by the high habitat quality within these forests. According to Akite (2008) the presence of forest edge species and species of wide occurrence in a forest sample give an indication of the extent of degradation of the forest. Rogo & Odulaja (2001) found high similarity between butterfly assemblages at the forest edges and forest interior at two degraded Kenya forest remnants, which was explained by low habitat quality at these forest patches and the presence of forest edge species at the forest interior. According to Collinge *et al.* (2002) patch characteristics are known to explain a greater proportion of the variation in abundance and species richness than do landscape characteristics.

The higher number of species trapped at Dlinza and Entumeni forest edge when compared to the forest interior was expected and would support our hypothesis 4 (Fig 22). This finding of a higher number of species in the forest edge would also be consistent with other studies. According to De Vries *et al.* (1997), the least disturbed habitat had the lowest butterfly species richness with the most disturbed (edge) habitats having the highest species richness. A similar trend was also found by Vu (2008) where the number of butterfly species increased from the natural closed forest to the forest edge, and then declined in the shrub layer and agricultural land. Therefore habitat edges are important for butterfly conservation, and this shows that human activities can have both positive and negative effects on the distribution of butterfly species and species richness (De Vries *et al.* 1997; White & Kerr 2007).

The higher mean species richness (d) at Dlinza forest interior when compared to the forest edge was also unexpected (Fig. 23a). This higher species richness (d) index could be partly due to the higher evenness (J) index of 0.834 at Dlinza forest interior when compared to the forest edge (Table 7). This may indicate a negative effect on Dlinza forest edge assemblages by the surrounding urbanization. Urban development poses a significant threat to many rare butterfly species, and has recently been at the center of a few high-profile butterfly conservation situations such as the Roodepoort copper *Aloeides dentatis dentatis*, the Brenton blue butterfly *Orachrysops niobe,* and Heidelberg Copper *Chrysoritis aureus* (Henning *et al.* 2009). Urbanization has also been reported in other regions of the world to be a significant factor driving the decline of butterfly diversity and abundance (Collier *et al.* 2006). Jana *et al.* (2006) found some Lepidopteran, Hemipteran, and Orthopteran species were susceptible to industrial pollution and therefore these orders can be valuable as bio-indicators. It has also been found in other regions that the Nymphalidae sampled by bait-traps are effective indicators of land-use change regardless of whether species richness or abundance was used (Barlow *et al.* 2007). The urban development and paved roadways surrounding Dlinza forest and consequently relatively high pollution may be contributing to the lower species richness (d) at Dlinza forest edge in comparison to the forest interior. Despite this fact, green areas in cities can contain a relatively high biodiversity and conservation value (Ockinger *et al.* 2009). These urban green areas can also play a valuable role in educating an increasingly urbanized population on biodiversity and conservation issues (McGeoch 2002).

A study in Japan at an urban green area reported the extinction of two herb or grass feeders due to the loss of stable grasslands due to deforestation (Ohwaki *et al.* 2008). At Dlinza forest the surrounding grasslands have been replaced by urban development and other land-use types. Exotic plant species may also be more abundant at this forest edge (De Kock 1991), and reduced species richness in disturbed habitats may be related to a greater relative abundance of exotic species (Kocher & Williams 2000; Henning *et al.* 2009).

The opposite trend at Entumeni forest of a significantly higher mean species richness (d) at the forest edge when compared to the forest interior was expected and would be due to the high habitat diversity adjacent to Entumeni forest edge such as large grasslands and small patches of indigenous vegetation (Fig. 23b). Tall high quality mixed-grasslands were found to have higher butterfly species richness than shorter lower quality grasslands (Collinge *et al.* 2002). Therefore the taller mixed grasslands surrounding Entumeni forest could be contributing to the higher species richness at the forest edge, and a higher abundance of certain species such as *P. dendrophilus indosa* and *B. safitza safitza*. The number of butterfly species in a certain area is strongly affected by the number of plant species (Kitahara & Watanabe 2003). This habitat adjacent to Entumeni forest also creates a mosaic effect which has been reported to result in higher species richness due to the formation of a new habitat at a boundary between neighboring patches (Natuhara *et al.* 1999). A study conducted in Japan also showed significantly higher butterfly species richness in forest edge sites when compared to the forest interior, with red list species and species vulnerable to extinction being observed more often in forest edge sites than forest interior (Kitahara & Watanabe 2003). This edge effect at Entumeni forest would also be consistent with a study undertaken at Muhaka and Mrima forest remnants in Kenya where the larger Mrima forest had a higher number of species at the forest edge (Rogo & Odulaja 2001).

A comparison of the mean Shannon diversity (H') index between forest interior and edge at individual patches showed some interesting trends. The higher mean Shannon diversity (H') index at Dlinza forest interior when compared to the forest edge was unexpected, and results in a partial rejection of our hypothesis 4 (Fig. 27a). This result could be partly explained by the higher evenness (J) index at the forest interior clearings. According to Vu (2008), a high evenness (J) index results in a higher diversity. This finding suggests that the forest edge assemblages at the smaller urban Dlinza forest reserve have been negatively affected by the surrounding urban landscape. However as previously mentioned many abiotic and biotic factors were not measured during the present study which could be contributing to the lower diversity at this urban reserves edge in comparison to the forest interior. This finding of a lower Shannon diversity (H') index at Dlinza forest edge would be an important contribution to knowledge for conservation authorities because although these fruit-feeding butterflies are reported in the literature to be resilient and less affected by habitat fragmentation than other butterfly groups they appear to be negatively affected by urban development (Uehara-Prado *et al.* 2007).

The higher mean Shannon diversity (H') index at Entumeni forest edge when compared to the forest interior was expected, and therefore supports our hypothesis 4 (Fig. 27b). This difference in diversity between forest edge and forest interior at Entumeni was however not significant. Other studies have found these edge effects of a significantly higher butterfly species diversity at the forest edge when compared with forest interior sites, however some of these studies may have included all butterfly groups and not only forest species (Kitahara & Watanabe 2003). However Vu (2008) found indices of evenness and diversity were low in the natural closed forest and highest in the forest edge where moderate disturbance had occurred. This would support the findings in the present study of a higher diversity at Entumeni forest edge. This high diversity at Entumeni forest edge highlights the importance of conserving forest edge habitats for the maintenance of butterfly species diversity (Vu 2008). This edge effect has been widely reported in the literature and is known to differ for certain species (Ries & Sisk 2008).

5.5 Comparison of fruit-feeding butterfly assemblages recorded in the Dlinza and Entumeni forests

Hypotheses 5 and 6 in the introduction (Chapter 1) are directly related to comparisons between the fruit-feeding butterfly assemblages of the two forests, Dlinza and Entumeni. Hypothesis 5 focuses on altitudinal differences between the two forests which are relatively small in the context of the regional landscape and may show limited differences such as reflected by more coastal versus more inland species. Hypothesis 6 supports the trend that Entumeni being the larger of the two forests and situated in a rural setting, will have a higher species richness and species diversity in comparison to Dlinza forest which is smaller and situated in an urban environment with higher anthropogenic influences at its edges. Similarities and differences in assemblage structure and species composition are considered to evaluate these hypotheses 5 and 6. A discussion of assemblage structure i.e. abundance, species richness and diversity of fruit-feeding butterflies of the Dlinza and Entumeni forests as well as the species composition of these assemblages follow.

The similar or slightly higher number of individuals trapped at the smaller Dlinza forest in comparison to the larger Entumeni forest, though not statistically significant, was unexpected (Table 7). However a study conducted in Brazil at forest fragments that ranged in size from 14 to 175 ha have shown no relationship between fragment area and abundance, and therefore the fruit-feeding butterfly guild is reported to be resilient and less affected by habitat fragmentation than other butterfly groups (Uehara-Prado *et al.* 2007). Fruit-feeding butterflies are also known to be adapted to naturally heterogeneous and disturbed environments which may mean they are less affected by anthropogenic disturbance (Uehara-Prado *et al.* 2007).

Studies involving butterfly population densities between forest patches of different sizes have been controversial in the literature. While one study found an unexpected significant decrease in butterfly densities with habitat area (Steffan-Dewenter & Tscharntke 2000), another study found species richness and overall abundance of Ithomiine butterflies in cloud forests did not depend on patch size (Muriel & Kattan 2009). A study by Krauss *et al.* (2003) found larger population sizes with increasing habitat area for both generalist and specialist butterfly species. This high butterfly abundance at the smaller urban Dlinza forest is important for butterfly conservation as this forest could act as a source population for re-colonizing other forest patches following extinction events. This high abundance at Dlinza forest also shows the significance of small urban reserves. Differences in population densities between forest patches can also be partially explained by immigration and emigration rates. There is a higher probability of dispersal to large forest remnants (Matter *et al.* 2005; Rabasa, Gutiérrez & Escudero 2007), while the emigration rate from smaller patches is higher due to a higher encounter with patch boundaries (Ries & Debinski 2001; Schultz & Cronje 2004). This trend would however contradict the findings in the first study period, but would be consistent with the findings of the second study period where the larger Entumeni forest had a higher overall abundance when compared to the smaller Dlinza forest.

The effect of altitude on arthropod abundance has also been reported in the literature. According to Wettstein & Schmid (1999) the abundance of several arthropods species which included butterflies and grasshoppers decreased significantly with increasing altitude.

Between forest patches, the higher abundance at Dlinza forest edge when compared to Entumeni forest edge could indicate a higher level of disturbance (Fig 20a). This is believed to be due to the difference in resources at Dlinza forest edge such as higher abundances of exotic plant species which results in the dominance and higher abundances of certain species. According to Ribeiro *et al*. (2008) the difference in resource distribution (host plants) among fragments could explain the high beta diversity. The lower evenness (J) index at Dlinza forest edge when compared to the forest interior would indicate the dominance of certain species. The reason for the higher number of individuals trapped at Entumeni forest interior in comparison to Dlinza forest interior could be due to a greater number of host plants and therefore the higher population densities at this larger forest interior (Fig 20b). Certain butterfly species such as *B. safitza safitza* and *E. hiarbas* had markedly higher numbers at the larger Entumeni forest interior. The higher abundance at Entumeni forest edge during the second study period of 2010 showed a different trend to the previous study period of 2009 (Fig 21a). However this second study was only a 3 month Autumn study and during Spring, Summer, and Autumn 2009 Dlinza forest had higher abundance at the forest edge which contributed to the higher abundance during the first 12 month study period (Fig.18). The higher number of individuals trapped at Entumeni forest interior during the second study of Autumn 2010 was consistent with the first study period (Fig 21b).

When comparing abundance at individual survey sites, resource distribution could explain the higher abundances recorded at DI3 and EI2 when compared to EE3 and the other interior survey sites (Tables 7, 8). Vegetation within these fragments is not homogeneous, but approaches a floristic mosaic of habitats with different composition of larval and adult resources resulting in concentrations of some species at sites where their resources are concentrated (Ribeiro *et al.* 2008). As the adults of these fruit-feeding butterflies feed on plant sap, butterflies may also tend to stay where this resource is more readily available (Ide 2000).

The lower abundance at DE3 in comparison to the other edge sites could be due to aspect (Table 7). DE1 and DE2 were located on the northern edge of the forest while DE3 had a south-eastern aspect. According to Ribeiro *et al.* (2008) orientation of forest fragments is important as more solar radiation during the year affects host plants and consequently the local fruit-feeding butterfly assemblages. A weak but significant positive correlation between light levels at trap locations and the mean number of butterflies trapped was also found in other similar studies (Lewis 2000).

The low abundance observed at the canopy survey site DI1 in Dlinza forest, could be partially explained by the low number of *Bicyclus safitza safitza* which is mainly an under-storey species and grass feeder (Fig. 37). This species made a marked contribution to abundance levels at most survey sites (Figs 37-40). Barlow *et al.* (2007) also reported trapping a lower number of butterflies at canopy survey sites in comparison to under-storey sampling sites in the Brazilian Amazon with no butterfly being a significant indicator of forest canopy assemblages. A higher number of *C. coranus coranus* was trapped at DI1 than other survey sites which may be an indication that this butterfly has higher numbers at canopy level (Fig. 37). Another possible explanation for lower abundance at this site could be disturbance to trapping as a result of people passing the trap when visiting the viewing platform, however this disturbance was thought to have no significant effect on the trapping at this survey point.

The higher number of species trapped at Entumeni forest was expected due to the larger forest size with higher habitat diversity (Tables 7, 8). This finding of a higher number of species at Entumeni forest supports hypothesis 6. Large habitats usually have higher habitat heterogeneity, and therefore a higher number of species (Steffan-Dewenter & Tscharntke 2000). This positive relation between butterfly species richness and habitat area has been found during other studies (Wettstein & Schmid 1999), however there are studies which show a different trend. For example, a study by Muriel & Kattan (2009) found species richness of Ithomiine butterflies in cloud forest fragments did not depend on patch size. A study in Africa by Larsen *et al.* (2009) also found a higher species richness at a smaller forest patch in Ghana, and suggested this was due to a landscape mosaic effect. Another study found species richness to be higher at fragmented woodlands (Natuhara *et al.* 1999). However generally it is well established that larger habitats have higher species richness. According to Akite (2008) forest sites that exhibit higher species richness are characterized by a variety of habitat that includes forest, grassland, and riverine or stream vegetation. This high habitat diversity is typically found at the larger rural Entumeni forest.

Some of the species contributing to the higher species richness at Entumeni were only captured once such as *C. jahlusa argynnides*, or had very low densities such as *J. terea elgiva* (Tables 3, 4). This higher number of low density species at Entumeni forest would be consistent with previous studies, which has found the species richness of specialist butterfly species to be higher in larger habitat patches (Krauss *et al*. 2003). According to Larson *et al.*

(2009) the butterflies *J. terea elgiva* and *P. tugela tugela* are unpredictable fruit-feeders, and this is supported by the low numbers trapped in the present study. An additional factor contributing to the higher number of species at Entumeni forest could be due to the higher elevation at Entumeni, which has been found in certain instances to be positively correlated with species richness however it was variables of habitat quality and not altitude alone which caused the observed changes (Wettstein & Schmid 1999). Recent studies also report an uphill shift in butterfly species related to climatic warming (Konvicka, Maradova, Benes, Fric & Kepka 2003; Storch *et al.* 2003). This global warming could be contributing to the higher number of species found at Entumeni forest, however due to the small difference in elevation between Dlinza and Entumeni forest it is believed that this factor is not important. Although Entumeni forest had a higher number of species during both study periods, this difference was not significant and 18 butterflies were common between the two forest patches (Tables 3, 4).

The reason for the higher number of butterfly species trapped at Dlinza forest interior in comparison to Entumeni forest interior is unknown as both forests are protected reserves and have similar habitat quality at the interior of the forest (Figs 33, 35). This finding could possibly be due to certain species avoiding the forest edge at Dlinza forest as a result of higher disturbance while at Entumeni the forest edge attracts more species.

It was expected that a higher number of butterfly species would be sampled at the larger rural Entumeni forest edge in comparison to the smaller urban Dlinza forest edge (Figs 34, 36). This finding could be due to the higher plant diversity at Entumeni forest edge, as species richness has been found to increase significantly with increasing diversity of the surrounding landscape (Krauss *et al.* 2003). According to the literature butterfly species declined in the agricultural land, and it is believed that the plant diversity at Dlinza forest edge is more homogeneous and similar in structure to the agricultural land than at Entumeni forest edge (Vu 2008). The results of the Autumn 2010 study were consistent with the first study and would highlight the importance of forest edges for butterfly species conservation (Figs 34, 36).

The low variation in overall mean species richness (d) found between the forests was unexpected due the smaller size of Dlinza forest, and the urban surroundings which were expected to have a greater adverse effect on the species richness (d) at this smaller urban forest reserve (Table 7). However forest fragmentation has been reported in other studies to have no significant effect on the species richness of fruit-feeding butterflies (Uehara-Prado *et al.* 2007). This finding could be partly due to the fact that Dlinza forest is relatively large, has high habitat quality, and has been established as a nature reserve for many years. This result indicates that in the present study habitat area had no significant effect on species richness. In fact certain species such as *J. terea elgiva, N. saclava* do occur at Dlinza forest but were not trapped. An additional butterfly *Hypolimnas anthedon* was trapped at Dlinza forest and not at Entumeni forest. Therefore the number of species common to the two forest patches is actually higher than the results show.

Between landscapes, the significantly higher mean species richness (d) at Entumeni forest edge when compared to the smaller Dlinza forest edge was expected and would be partly due to the high habitat diversity adjacent to this larger forest reserve (Fig. 24a). Despite the higher evenness (J) index at Dlinza forest edge when compared to Entumeni forest edge, a higher number of butterfly species were trapped at Entumeni forest edge. This higher habitat diversity would result in the trapping of rarer and low density butterfly species such as *C. jahlusa, B. ilithyia, B. anvatara acheloia, S. natalensis* and *J. terea elgiva* which were unique to Entumeni forest edge and were not trapped at Dlinza forest edge (Figs 34, 36).

Surprisingly Dlinza forest interior had a higher mean species richness (d) when compared to Entumeni forest interior assemblages (Fig. 24b). This could be due to the dispersal of specialist butterfly species to the forest interior at Dlinza as a result of anthropogenic influences at the forest edge such as a higher abundance of exotic plant species and a higher use of pecticides in the urban surroundings. This relatively high species richness recorded at Dlinza forest interior may also be due to the relatively large size of this urban forest reserve, and it is believed that if the Dlinza forest reserve was significantly smaller the effect of the surrounding landscape on the interior butterfly assemblages would be more profound. According to Collinge *et al.* (2002) as patch size declines the effect of urbanization will be stronger.

Having found a similar trend in the second study during Autumn 2010 of higher mean species richness (d) at Entumeni forest edge when compared to the forest edge at Dlinza, and higher species richness (d) at Dlinza forest interior in comparison to the Entumeni forest interior confirms the previous findings and would appear to indicate a negative effect on the assemblages at Dlinza forest edge (Fig. 25). This highlights the value of forest edges for butterfly conservation. The higher mean species richness (d) at Entumeni forest edge during the second study was however not significant as it was during the previous year. These forest edges need to be preserved as they show higher species richness, and where possible buffer zones should be planted to protect these edge assemblages from the effect of urban development.

When comparing the number of species trapped at individual survey sites the higher number of species trapped at DE2 when compared to the other two forest edge sampling sites could be explained by the location (Table 7). This sampling site was the furthest from a paved roadway. Paved roadways may have a negative effect on butterfly assemblages, such as differences in temperature, the reflective nature of the road (Ries & Debinski 2001), or air pollution from vehicle traffic. An increasing extent of paved roads is associated with reduced butterfly species richness reflecting habitat fragmentation or particularly severe habitat loss associated with urbanization (White & Kerr 2007).

The forest edge survey site which was the closest to a paved roadway at Dlinza forest was DE3. This survey site had the lowest number of species in comparison to the other forest edge survey sites for both study periods (Tables 7, 8). However DE3 also had a cooler southeastern aspect which could also possibly have resulted in a lower number of species being trapped at this survey point.

Large high quality habitats are important for insect diversity conservation (Steffan-Dewenter & Tscharntke 2000; Samways 2005; Kobayashi *et al.* 2008), and are known to be valuable for the preservation of rare and endemic butterfly species (Horner-Devine *et al.* 2003; Ockinger & Smith 2006).

The overall higher mean Shannon diversity (H') index found at the smaller urban Dlinza forest was unexpected, and as a result our hypothesis 6 is partially rejected (Fig. 26). There are conflicting reports in the literature regarding diversity and habitat area. For example, while Steffan-Dewenter & Tscharntke (2000) found the diversity of grassland butterflies were positively correlated with habitat area, a study by Muriel & Kattan (2009) found small habitat patches had higher diversities than large patches and suggest other factors that operate at different spatial scales may be influencing butterfly diversity in the forest patches. In Japan Natuhara *et al.* (1999) found slightly lower diversity indices in fragmented woodlands when compared to non-fragmented woodlands. A study in South Africa on various pollinator species showed no significant difference in the Shannon diversity (H') index between patches of different sizes, and found small patches of < 1ha contained a high diversity and that species were more sensitive to habitat characteristics than to fragment size (Donaldson *et al.* 2002). This result of a higher overall mean Shannon diversity (H') index at the smaller Dlinza forest could be partly due to the Shannon diversity index giving more weight to common species than to species richness (Ribeiro *et al.* 2008). Dlinza had a higher butterfly abundance, and there were uncommon and low density species which were only trapped at Entumeni forest and not at the smaller urban Dlinza forest (Tables 3, 4). This result highlights the value of smaller forest patches, even those in urban environments. However as Dlinza forest is relatively large at 250 ha further studies at smaller forest fragments should be conducted to be able to arrive at clearer conclusions. The Dlinza forest may exceed the minimum viable area (MVA), and be large enough to support the fruit-feeding butterfly populations.

Between forest patches the higher mean Shannon diversity (H') index at Entumeni forest edge in comparison to Dlinza forest edge was expected (Fig. 28a). Although not significant, this higher species diversity at Entumeni forest edge may be as a result of a high habitat diversity surrounding Entumeni forest reserve such as large grasslands and patches of indigenous trees, and the possible negative impact of the urbanization surrounding Dlinza forest on this forests edge assemblage. According to Akite (2008) the degree of habitat disturbance is an important factor that determines species diversity and composition of a given habitat. Benedick *et al.* (2006) found beta diversity between sites was significantly related to the difference in vegetation structure. Although these two forest patches have similar vegetation communities it is believed there is a marked difference in plant diversity between these two forest edges as a result of anthropogenic influences.

Surprisingly, Dlinza forest interior had a higher diversity when compared with Entumeni forest interior (Fig. 28b). Although this difference was not statistically significant, this observation highlights the importance of urban habitats for biodiversity conservation. In regions dominated by intensive land use, cities can contain a relatively high biodiversity and conservation value (Ockinger *et al.* 2009). This observation of a higher diversity at Dlinza forest interior could be as a result of the surrounding landscape characteristics such as higher exotic species which negatively impacts the butterfly assemblages at the smaller urban Dlinza forest edge resulting in an overall higher diversity at the interior of Dlinza forest.

The second study period showed a similar trend as the first study (Fig. 29). The mean higher Shannon diversity (H') index at Entumeni forest edge when compared to Dlinza forest edge, and the mean higher diversity at Dlinza forest interior in comparison to Entumeni forest interior is consistent with our first study and confirms the importance of forest edge landscapes and would suggest the fruit-feeding butterfly group is valuable as biological indicators in showing anthropogenic disturbance (Uehara-Prado *et al.* 2007).

When comparing individual assemblages the higher Shannon diversity (H') index at DI1 was not expected due to the relatively low abundances recorded at this canopy survey point, however this observation could be the result of a reported vertical stratification of fruit-feeding butterfly assemblages as found by some authors (Walla *et al.* 2004; Uehara-Prado *et al.* 2007) (Tables 7, 8). This survey site is shown as an outlier at Dlinza forest (Fig. 26). It could be interesting for future studies to include more canopy survey points however logistically this would be difficult as bait-traps are easily deployed at or near ground level. Lehmann & Kioko (2000) also pointed out that the species list in Kenyan forests may have been incomplete because certain species such as *Pseudathyma lucretioides lucretioides* have a reputation for staying at tree-top level and rarely descend. Others may stay lower down for example in the present study as two *Pseudacraea lucretia tarquinea* were trapped at EI3 which was an under-storey survey point, while only one individual was trapped at DI1 which was a survey site in the canopy (Figs 39.3, 37.1). A larger series of data for this species may point to an actual preference to different stratums in the forest.

In a DCA ordination of survey points and species recorded at Dlinza and Entumeni forests for the first study period of June 2008-May 2009, two compact closely associated groups of survey sites in the ordination graph of Dlinza and Entumeni assemblages indicate there are differences in species composition between the two forests, however the differences are minimal (Figs 30). The widely separated survey points in the ordination space show unique variation in species composition during certain seasons.

The separation of EI3 during spring and winter was due to the capture of infrequent species such as *N. saclava* and *P.lucretia* during spring, and *P. lucretia* during winter. EE3 during summer and winter also included Nymphalid species which were not regularly captured in the bait traps such as *C. cloanthe cloanthe, H. perspicua, J. tugela tugela and C. zoolina,* and these assemblages also had high similarity in species richness during these seasons. *C. zoolina zoolina* was trapped at E11 during winter, while EE1 during winter had species present such as *C. cloanthe cloanthe, H. perspicua, C. druceanus druceanus* and *C. zoolina zoolina*.

DI2 during winter included species such as *C. coranus coranus* and *P. tugela tugela* which could explain the variation of this site, while during autumn the highly seasonal Satyrine *P. dendrophilus* was trapped. DI1 during summer and autumn had a close association which was due to high similarity in species composition. This survey point had six species in common during both seasons, and during autumn DI1 had a significantly higher species richness as well *P. lucretia* and *S. boisduvalli* which were uncommon in the bait traps which would explain its higher variation. The trapping of *N. laeta* at DE3 during winter could explain this forest edge site showing variation.

The relatively close grouping of Dlinza and Entumeni forest survey points indicates high similarity in species composition for many survey sites of the two forests, however some survey points show high variation in species composition (Fig. 31).

The wide separation of a Dlinza edge survey point could be the difference in species composition and lower light levels at DE3. There are also survey points within each forest which have very similar species composition such as Dlinza interior surveys points, Entumeni edge points, Dlinza edge assemblages, and Entumeni interior sites (Fig. 31).

There are also high similarities during certain seasons between survey sites of both forests such as Dlinza interior sites and Entumeni edge sites, Dlinza edge and Entumeni interior sites.

5.6 Species ordination

The group of species on the left of the graph such as *M. leda*, *B. anynana, C. cloanthe cloanthe, C. zoolina zoolina, H. perspicua* were seldom caught and had low abundance throughout the duration of the study (Tables 3, 4). The middle grouping of species consisting of *C. cithaeron cithaeron, C.candiope candiope, C. ethalion ethalion, B.safitza safitza, E. hiarbas angustata,* and *C.varanes varanes* showed high abundance at both forests and were among the most dominant species trapped (Tables 3, 4). The species at the top of the graph consisting of *P. dendrophilus, C. xiphares peningtoni, C. jahlusa argynnides, C. brutus natalensis, and C. druceanus, druceanus* showed strong seasonal variation in abundance and were mostly flying during autumn (Figs 41, 42).

The grouping of species to the right of the ordination graph such as *N. laeta, N. saclava, P. lucretia, C. coranus coranus, S. natalensis, J. terea elgiva, P. tugela tugela* were also low density species and several of these butterflies were only trapped once (Tables 3, 4).

5.7 Species responses

The high number of butterfly species common to both forest patches was not expected (Tables 3, 4). However, these two forests have similar vegetation communities (Mucina *et al.* 2007), which is known to result in similar butterfly diversity (Vu 2008). The influence of vegetation types in Charaxinae distribution is also considerable, for most Charaxinae species are more or less habitat specific (Henning 1989). Therefore our findings of 8 *Charaxes* species common to Dlinza and Entumeni forests would be consistent with the literature. The significantly higher abundance of *C. cithaeron cithaeron* and *C. varanes varanes* at the smaller Dlinza forest can be due to several reasons. Firstly, these butterflies are reported to be mainly of coastal lower altitude forests (Woodhall, 2005). Secondly, the vegetation surrounding the smaller fragmented Dlinza forest may be more suitable for these butterfly species. *C. varanes varanes* is mainly a forest edge species (Woodhall 2005), and one of its host plants *Allophylus africanus* occurs on forest margins (van Wyk & van Wyk 1997). A study in the Brazilian Atlantic forest by Uehara-Prado *et al.* (2007) also found significantly higher numbers of Charaxinae and Biblidinae in fragmented forest patches when compared with a large contiguous habitat, and link this with the use of host plants which are mainly edge species favoured by fragmentation. These findings were also consistent with a study in South Africa which found that the response of pollinator species to different patch sizes was species specific (Donaldson *et al.* 2002). There have also been reports in the literature of a correlation between Butterfly body size and habitat area, with larger bodied species more adversely affected by habitat fragmentation than smaller butterfly species (Benedick *et al.* (2006). This would be inconsistent with the present study as the Charaxinae had higher representation at the smaller Dlinza forest (Fig. 12).

The difference in abundance of *C. xiphares penningtoni* between the two forests has also been previously mentioned in the literature, with De Kock (1991) finding this butterfly to be scarce at the smaller Dlinza forest and more abundant at the larger higher altitude Entumeni forest. During our study however a higher abundance of this butterfly was recorded at Dlinza forest (Tables 3, 4). This could be explained by previous surveys being of short duration which did not give an accurate reflection of this butterfly composition between the two forest patches.

The species similarity between Dlinza and Entumeni forests highlights the importance of small fragmented forest patches for forest butterfly conservation even those patches in an urban environment (Tables 3, 4). However, the similarities may be higher than the data shows, as several of the species recorded in the species list as being unique to Entumeni forest such as *M. leda, N. saclava, J. terea elgiva* do occur at the smaller Dlinza forest. These butterflies were either not trapped or were omitted from the statistical analysis due to standardization of the data. The trapping of certain species such as *C. jahlusa argynnides, S. natalensis* which were unique to Entumeni forest was expected due to the higher habitat diversity at Entumeni forest. However fruit-feeding butterflies are reported to be affected by forest fragmentation as cluster analysis and CA segregated the larger forest reserve and fragment sampling units into two distinct groups indicating that habitat fragmentation does have an effect on the fruit-feeding guild and that this effect may extend beyond the species richness (Uehara-Prado *et al.* 2007).

The high number of species which were common to Dlinza forest interior and edge was unexpected, as many studies have found marked differences in species richness between these two forest habitats (Figs 33, 34). The butterflies *C. varanes varanes, and B. safitza safitza* had markedly higher numbers at Dlinza forest edge, and this would be consistent with the literature where they are reported to be forest edges species (Woodhall 2005). However, a study in Vietnam by Vu (2008) found butterflies from the subfamily Satyrinae had higher numbers at the forest interior in comparison to the forest edge. Their findings would not be consistent with the results in the present study where higher numbers of *B. safitza safitza* and *P. dendrophilus* were trapped at Dlinza forest edge (Fig 34). Host plants of these butterfly species are from the family Poaceae which could explain its high number at the forest edge near the grasslands, or where more sunlight is available. In tropical forests different interior versus forest edge patterns in distribution of Satyrinae may be present.

Eight of the nine Charaxinae species trapped at the two forests in our study area are reported to be forest edge species (Woodhall 2005), based on experience of lepidopterists, which would explain the observation that more than 60% of butterflies from this subfamily were trapped at the forest edges (Figs 34, 36). *C. coranus coranus* is reported to be a forest edge butterfly (Woodhall 2005), therefore the higher abundance of *C. coranus coranus* at the forest interior would not be consistent with present literature. An explanation could be the higher number of *C. coranus coranus* trapped at DI1 and the open glades at the interior of these forests which create a similar environment to the forest edge (Fig. 37.1). Although these two reserves are closed canopy forests and of high quality, open forest patches do occur at the forest interior. The higher abundance of *E. dryope* at the forest edge would be consistent with the literature (Woodhall 2005).

The higher number of species which were unique to Entumeni forest edge would be expected due to the higher habitat diversity surrounding this forest such as the grasslands and small forest fragments (Fig. 36). Several studies have found low density and rare butterfly species in the forest edge (Kitahara & Watanabe 2003). Most of the 8 species unique to Entumeni edge are forest edge species (Woodhall 2005). The butterfly *C. cloanthe cloanthe* is reported in the literature to be common in the grasslands therefore a higher abundance of this butterfly at the forest edge would be expected (Woodhall 2005). The trapping of a single *C. jahlusa argynnides* at Entumeni forest edge was a rare event as this species is reported to be common in the savanna and lowland forest (Woodhall 2005). The high species richness at Entumeni forest edge would indicate intermediate disturbance which is reported to result in a higher species richness (Vu 2008). *C. ethalion ethalion* was clearly more abundant at the larger Entumeni forest edge, and this is thought to be due to the higher host plant abundance at this forest edge.

There were 14 species common to both forests during the second study (Table 4). This relatively high number of butterfly species common to both forests is important when considering the difference in size of these forest remnants and the urban development surrounding Dlinza forest reserve which was expected to have a significant effect on the species richness at this urban forest patch.

The low abundance of *B. safitza safitza* was expected at DI1 in Dlinza forest due to the position of this bait-trap in the canopy (Fig. 37.1). According to Woodhall (2005), *E. hiarbas* *angustata* is also a forest edge species and more abundant at higher mountainous areas which would explain its high numbers at EE2. The relatively high numbers at EI2 could be due to resource distribution.

There were clear seasonal patterns observed at the forests for certain butterfly species such as *P. dendrophilus, C. xiphares peningtoni,* and *C.brutus natalensis* (Figs 41-43). It is therefore recommended that any future studies include all four seasons especially winter and autumn as these two seasons show the highest abundance and species richness in the present study.

5.8 Importance of conservation of forest patches and its butterfly assemblages

Prospects for conservation of the forest ecosystems in Africa are bleak due to the unprecedented population explosion in the tropics (Henning 1989). According to McGeoch (1993) an understanding of anthropogenically induced effects on invertebrate communities is essential if an attempt is to be made to reduce the impact of human activity and conserve biodiversity, and this should be the primary goal of all conservation efforts. However, in many African countries, invertebrates are mainly excluded from conservation planning, biodiversity conservation and management activities (Akite 2008). It has been found that the major or only factor in the loss or decline of insect populations throughout the world is habitat destruction (Henning 1989). Although the *Charaxes* species which was by far the dominant species trapped during this study are in general not as endangered as most other butterflies and are also fairly widespread (Henning 1989), their habitat is under threat as forests in KwaZulu-Natal are under immense pressure, and are dwindling at an alarming rate (Wager 1976). The most severely affected areas of indigenous forest in South Africa are along the coast of Natal, and in the major areas perhaps over 90% of the original forest has been cleared for agriculture (mostly sugarcane), urbanization, and industry (Cooper 1985).

Since the overall aim of this study is to contribute to knowledge which will enhance the conservation of indigenous forests in the KwaZulu-Natal province South Africa, and their associated forest butterflies, present results highlight the importance of small forest patches. Results also indicate that for regional butterfly conservation small forest remnants are crucial and make a significant contribution to the biodiversity of a region. However the trend at Dlinza forest is a negative impact on the butterfly assemblages at the forest edge. Therefore where possible urban development should be avoided or reduced near these forest ecosystems or if this is unavoidable buffer zones should be provided to offset the apparent negative effect on these edge assemblages.

In other areas of the world similar results have also been found. A study by Benedick *et al.* (2006) found certain species in small forest remnants which were absent or had low numbers in the larger forest reserve. While some butterflies are able to adapt to this rapidly changing world, many will be lost (Henning 1989).

Most forest butterflies depend on high quality forest for their survival and are reluctant to disperse to new habitats (Larsen 1991). Butterfly range expansions have also been reported in certain areas of world due to climatic warming. These forest butterflies will therefore be under greater threat of extinction unless the remaining forest patches are preserved to allow dispersal and prevent genetic loss from inbreeding and genetic drift.

Minimum viable populations (MVP) and areas have not yet been established for any South African butterfly species (Terblanche & Edge 2007). With the probability of extinctions increasing with decreasing population size (Begon *et al.* 1996) and area (Krauss *et al.* 2003), it is crucial to gather not only qualitative but also abundance data on butterfly assemblages. With habitat fragmentation being one of the most important contributing factors to butterfly extinction the remaining forest remnants are needed as stepping stones and dispersal corridors. However it should be emphasized that in order to maximize forest butterfly conservation, it would be desirable to preserve other forest types, which because of their difference in vegetation, may have other *Charaxes* subspecies present. Forests in South Africa are often present as fairly isolated pockets at different altitudes and latitudes which favour the evolution of subspecies.

CHAPTER 6: CONCLUSION

The main aim of the study is to acquire knowledge that will enhance the conservation of butterfly assemblages as well as future research about butterfly assemblages in African forest patches. For this reason fruit-feeding butterfly assemblages of two KwaZulu-Natal forests, Dlinza and Entumeni, were chosen as the focus of this study. A wealth of general knowledge exists on South African butterfly fauna. Much of this large body of knowledge was gained from a rich history of experience in the field by numerous enthusiastic lepidopterists. However, a huge challenge and a large gap in this knowledge about South African butterflies are to address the lack of comparable data yielded by quantitative studies in the field. For example butterfly fauna at the Dlinza and Entumeni forests are fairly well-known, but patterns of butterfly assemblages in different seasons of the year and how these butterfly assemblages respond to forests edges and forest interior clearings are poorly explored. Biodiversity studies are by nature multifaceted and as a consequence a number of hypotheses have been evaluated. Even the appropriateness of the technique itself, of counting butterflies with the aid of baited traps, had to be evaluated for the two forests, some distance, more than 28° S latitude, from the equator.

The current study had several objectives, mainly based on hypotheses:

- To assess the effectiveness of the *Charaxes*-bait trap as a survey technique for trapping and studying these butterfly species,
- To investigate the dispersal patterns of fruit-feeding butterflies at the Dlinza and Entumeni forest reserves,
- To study the seasonal responses of fruit-feeding butterfly assemblages at the Dlinza and Entumeni forests,
- To compare fruit-feeding butterfly assemblages between forest interiors and edges and between the two forests, Dlinza and Entumeni,
- To assess possible responses of these fruit-feeding butterfly assemblages to habitat area, altitude, and urban development at the forest edge. This assessment was based on comparisons of assemblage structure which include abundances, species richness and diversity as well species composition of assemblages.

Based on research findings which are outlined above two more objectives follow:

- To give a description of the fruit-feeding butterfly assemblages at the Dlinza and Entumeni forests,
- To note implications for conservation and also give recommendations for conservation of these forests and its butterfly assemblages.

Baited traps ("*Charaxes*-traps") that use bait consisting of a simple standardised concoction of fermenting bananas, pineapple, sugar and yeast are effective as a survey technique for trapping and studying the fruit-feeding butterfly species in the KwaZulu-Natal forests. Though the abundance and number of species recorded at the two forests are markedly lower than other tropical areas of Africa, the results with this technique exceeded the expectations. Approximately 33 % which this fruit-feeding butterfly assemblage contributes to the overall presently known butterfly species at these forests is substantial and suggest that this fruit-feeding guild maybe important in monitoring environmental changes in future. It is therefore recommended that this survey technique be included in any future study or environmental conservation planning for forests and forest butterflies in the southern African sub-region. Future sampling could include deploying bait-traps at forest canopy level, as the literature shows marked differences in the vertical stratification in some butterfly species, and the present study would appear to support these findings. Because only one survey point was used at canopy level, additional surveys at canopy level would need to be conducted to confirm this theory at Dlinza and Entumeni forests. Another factor to consider, although difficult for certain areas due to trap disturbance, could be to extend the effective daily capture time by leaving bait-traps in position for a longer period which may see higher numbers captured for certain species such as *M. leda* which is a species that is active later in the day or even at dusk.

The hypothesis about the mark-release-recapture procedure in the introduction (Chapter 1) stated that a moderate turnover of species was expected which may imply moderate abundances of species, with a lesser turnover at the smaller Dlinza forest. From the unexpected but decidedly low number of recaptures recorded at both forests in this study it is clear that these forests are capable of supporting a high turnover of fruit-feeding butterfly species and that the smaller Dlinza forest also supports a high turnover of species. Owing to the low number of recaptures recorded at Dlinza and Entumeni forests, the fruit-feeding butterfly populations have a high turnover of species, are stable, and under no immediate threat of extinction as long as the forest habitat is conserved. Recaptures were all stay at home events and the possibility that dispersal events are very rare should be researched further. Possible rarity or lack of dispersal between forest remnants is noted, and this could be problematic for conservation issues such as gene-flow and the maintaining of meta-population structures. Dispersal events may have gone undetected, as studies in other parts of the world report dispersal events of several kilometres whilst in the present study the Dlinza and Entumeni forests are only 7km away from each other. W.S. Forrester made some anecdotal observations of *Charaxes* species flying over sugarcane fields far from apparent suitable forest habitats. *Charaxes* species are strong fliers (Henning 1989) and mark-release-recapture surveys in the study area which could include smaller forest pockets between larger forest patches could shed more light on dispersal of these fruit-feeding butterfly species in the region.

Time of the year is critical to many insect ecology and conservation studies (Samways, McGeoch & New (2010). This study has showed that autumn and winter are optimum periods for trapping fruit-feeding butterflies at these forest patches, and any limited or once-off surveys should include these months. Though autumn was predicted correctly in hypotheses 3 of the introduction (Chapter 1) as an optimal time of the year to survey fruit-feeding butterflies in the Dlinza-Entumeni part of the region, the productiveness of the winter months was underestimated. Regionally this optimal time may shift at the higher altitude forests closer to the escarpment of KwaZulu-Natal South Africa. Having optimal periods for surveys of a diverse group of showy insects, creates opportunities for dividing workloads during the year in terms of forest invertebrate surveys.

A significant finding to emerge from this study was although the number of butterfly species trapped was higher at both forest edges when compared to the forest interior, the smaller urban Dlinza forest reserve had higher indices of species richness (d) and Shannon diversity (H') at the forest interior while at Entumeni forest these indices were higher in the forest edge. This finding would suggest that urban development at Dlinza forest edge probably has a negative impact on these fruit-feeding butterfly assemblages. As this study was of an explorative nature it is recognized that reasons behind these patterns are complex and require further investigation. Adverse effects on fruit-feeding butterfly assemblages at forest edges could include higher prevailing temperatures, pesticide levels, and higher densities of exotic species. Further studies should include considering different environmental factors such vegetation studies at the forest fringe. For example at Entumeni, *Allophylus* species and creepers such as *Senecio* are dominant along the forest margins (Louw, pers. comm., 2011). One of these two plant genera conspicuous at the edge of the Entumeni forest, *Allophylus*, contains larval host plants of *Charaxes brutus natalensis* and *Charaxes varanes* (Henning 1989; Appendix 1). Several other studies have shown the fruit-feeding butterfly guild to be useful as biological indicators.

Altitude had no significant effect on overall mean abundance, species richness (d) and Shannon diversity (H') index. Surprisingly species composition was also very similar between the two forests, consistently at the different seasons during a year. This finding was expected in one of the hypotheses of the introduction (Chapter 1) which could largely be ascribed to the small difference in altitude between these two forest patches and their close proximity. Forest patches which are further away and are at higher altitudes are expected to have different vegetation communities and therefore will have different *Charaxes* subspecies.

One of the more significant findings to emerge from this study was that the Entumeni forest had higher species richness, and the smaller Dlinza forest had a marginally higher Shannon diversity (H') index, which was unexpected. During the first 12 month study period the smaller urban Dlinza forest had a higher mean butterfly abundance, and a marginally higher Shannon diversity (H') index, while the larger Entumeni forest had a slightly higher species richness (d) index. The higher abundance and diversity, at Dlinza forest was unexpected due to its smaller size when compared to Entumeni forest and location in an urban environment. If not statistically significant this higher abundance and diversity of fruit-feeding butterfly assemblages at Dlinza are at least similar or marginally higher. This finding could be as a result of the relatively large size (250 ha) of this forest and high habitat quality. However, the present study showed that Dlinza forest is large enough to support relatively large populations of these forest butterflies. As the forest is a nature reserve and well established this is also thought to play a significant role in the higher diversity at this forest patch. Further studies need to be conducted at smaller forest patches to determine the critical size which will have an adverse effect on these butterfly assemblages in this region. The higher species richness (d) index at Entumeni was expected due to its larger size and higher habitat diversity at this forest.

A number of characteristics of the fruit-feeding butterfly assemblages were identified through comparing fruit-feeding butterfly assemblages in forest interiors and forest edges and also between the Dlinza and Entumeni forests. The fruit-feeding butterfly assemblages at Dlinza and Entumeni forests have been described in detail in the discussion.

Overall, the Charaxinae, Biblidinae, and Satyrinae were the most dominant subfamilies represented at the Dlinza and Entumeni forest reserves. Of the 9 *Charaxes* species found at these two forest reserves the species with the highest abundance were *C. candiope, C. brutus, C. xiphares, C. varanes, C. cithaeron, and C. ethalion*. Many of these butterflies had higher abundance in the forest edge which once again highlights the value of forest edges and surrounding landscapes for biodiversity conservation. The abundance of the Charaxinae was also lower in the canopy at DI1.

From the Biblidinae *E. hiarbas* and *E. dryope* showed highest abundance, and were also predominantly trapped at the forest edge. There was a markedly high number of *E. hiarbas* trapped at the larger rural Entumeni forest edge. This could be attributed to a higher abundance of this species host plant at the forest edge. Butterfly species trapped from the subfamily Satyrinae were mainly *B. safitza* and *P. dendrophilus*. *B. safitza* is abundant throughout the year in all four seasons, while *P. dendrophilus* is mainly trapped in autumn months and therefore is strongly seasonal.

Ultimately the overall aim of this study was to contribute to knowledge which would enhance the conservation of indigenous forests and its associated butterfly fauna in South Africa. It is trusted that the findings of this study confirm, strengthen and add new knowledge on several aspects of forest butterfly conservation and the conservation of forests in the region. A number of recommendations for further research and conservation management emerge from this study:

6.1 Research recommendations

- Using baited traps to study fruit-feeding butterflies in South African forests is rewarding in terms of quantitative results and should be pursued further,
- Mark-release-recapture procedures show that a high turnover of abundances of fruit-feeding butterfly assemblages are present in at least some South African

forests, but incidences of dispersal within and between forests deserve much more research,

- Studies on forests over a wider range than the present study should follow, and may due to time and logistic constraints focus on forest edges, which have been very productive in this study,
- Quality of the grassland-forest ecotone should be researched in detail, because a grassland buffer may even have an effect on true forest butterflies,

6.2 Conservation management recommendations

- Forest pockets in between larger forest patches could be very important for dispersal and act as stepping stone corridors for butterfly conservation. An ecological management plan should be compiled for such pockets, which should be continuously updated by more research. Landowners, conservation officials, communities and their leaders, agricultural institutes and non-governmental organisations should be aware and apply such ecological management plans in a coordinated effort.
- Alien plant species should be eradicated as far as possible in the forest environment, because these alien invasive plant species not only occupy suitable habitat in general, but also indigenous larval host plants of forest butterflies in particular,
- Alien plant densities, often the highest along the forest margin or ecotone should be controlled in particular along these forest margins (edges). If alien plants were not eradicated, fire would pose an enormous threat to the forest margin and also the forest interior. In a sense, the forest margin is the forest buffer, against alien plant establishment within the forest interior, reducing wind speed which minimises drying out. Forest margins are dynamic and able to move during both wet and dry years ([1]Louw, pers.comm., 2011).
- The Invasive Alien Species Programme established by Ezemvelo, KwaZulu-Natal which addresses alien plants protected areas is to be commended. The indigenous heritage contained in the natural forest patches cannot afford any lack of funds

budgeted. Also the eradication of alien invasive species should be extended to private land owners, large private or parastatal agricultural companies and industries.

- Tree harvesting should be limited and managed. For example at the Nkandla forest a decline in the abundance of *Ocotea bullata* has caused its substitution with *Pterocelastrus rostratus* by local harvesters (Scott-Shaw, pers. comm., 2006).
- Buffer zones of grasslands adjacent forests should be as large as possible, at least a few hundred metres, with perhaps a minimum of 30m within the urban edge where developments have already taken place,
- Buffer zones consisting of the grassland-forest ecotone of the Dlinza and Eshowe forest edges need to be restored or at least be rehabilitated where restoration is not feasible,
- No residential or industrial developments should be allowed at the edge of the forest, and should in particular not influence the natural forest-grassland ecotone,
- Structures inside forests should be limited to a minimum, although the well controlled viewing tower at Dlinza, benefits conservation awareness of not only birds and plants, but also forest butterflies, enormously. More available information on the butterflies and their dependence on such forests habitats could add value to the present conservation awareness efforts which focus a lot on forests vertebrates (birds, small mammals) and plants. This viewing tower may also aid research on the stratification in forest butterfly assemblages of South Africa.

Often the world's attention and conservation efforts are focused on the larger charismatic mammals and rightly so, however let us not neglect to preserve and understand the smaller more inconspicuous animals such as butterflies and the magnificent forest ecosystems upon which all life depends. Walking through a tropical rainforest without seeing a butterfly would be like swimming over a coral reef without seeing the striking colours of an angel or clown fish. In addition to their aesthetic appeal, these butterflies have also shown in this particular study to be valuable as biological indicators and therefore they can teach us much about the environment in which we live.

CHAPTER 7: REFERENCES

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CHAPTER 8: APPENDIX

a) List of Butterfly species and their associated larval host plants

A summary of the fruit-feeding butterfly species trapped at Dlinza and Entumeni forests indicating their subfamily, and associated larval host plants. The literature sources used were, Henning (1989)[1], Pringle, Henning & Ball (1994)[2], Williams (2011)[3].Host plants listed here not differentiated for subspecies or different regions (countries of the Afrotropical region).

Species	***Subfamily***	***Larval Host Plant***
1) *Charaxes brutus natalensis*	Charaxinae	*Allophylus* sp.[1], *Blighia unifugata*[1], *Ekebergia benguelensis* [2], *E. capensis*[1,2], *Entandrophragma delevoyi*[1], *Grewia forbesi* [1],*Khaya nyasica*[1,2], *Lepidotrichlia volkensii* [1],*Melia azedarach*[1,2], *Securinega virosa* [2,3], *Trichilia dregeana*[1,2],*T.emetica*[1,2],*Turraea floribunda*[1,2], *T. nilotica*[1],
2) *Charaxes candiope candiope*	*Charaxinae*	*Croton dichogamus*[1],*C. gratissimus* [1,2], *C.macrostachys* [1,2], *C. megalocarpus* [1],*C. sylvaticus*[1,2]. *These are from the family Euphorbiaceae.*
3) *Charaxes cithaeron cithaeron*	*Charaxinae*	*Afzelia quanzensis* [1,2], *Albizia adianthifolia* [1,2], *Baphia racemosa* [1,2], *Celtis africana* [1,2], *Chaetachme aristata* [1,2], *Cola laurifolia* [1],*C. natalensis* [1,2], *Craibia brevicaudata* [1],*C. brownii* [1], *Dalbergia lactea* [1], *Deinbollia kilimandscharica* [1], *Grewia sp* [1],*Hippocratea Africana* [1],*Hugonia orientalis* [1,2], *Leptoderris sp* [1],*Maytenus senegalensis* [1,2],*Melletia sutherlandii* [1,2], *Trema orientalis* [1,2].
4) *Charaxes druceanus druceanus*	*Charaxinae*	*Bersama abyssinica, Syzygium cordatum* [1,2], *S. gerrardii* [1], *S.guineense* [2].
5) *Charaxes ethalion ethalion*	*Charaxinae*	*Acacia ataxacantha* [1,2], *A.kirkii* [1,2], *Albizia adianthifolia* [1,2], *A. coriaria* [1], *A. gummifera* [1], *Amblygonocarpus andongensis* [1], *Cathormoin altissimum* [1],*Dalbergia lacteal* [2], *Dichrostachys cinerea* [1,2], *Entada abyssinica* [2],

		Mimosa pigra [1,2], *Newtonia buchananii* [1,2], *Parkia filicoidea* [1],*Peltophorum africanum* [2], *Pseudoprosopis fischeri* [1],*Scutia myrtina* [1,2], *Tamarindus indica* [1,2].
6) *Charaxes jahlusa argynnides*	*Charaxinae*	*Dalbergia melanoxylon* [2], *Haplocoelum foliosum* [1,2], *Lecandiodiscus fraxinifolius* [2], *Pappea capensis* [1,2].
7) *Charaxes varanes varanes*	*Charaxinae*	*Allophylus africanus* [1,2], *A dregeanus* [2], *A. glaucescens* [1], *A. macrostachys* [1], *A. melanocarpus* [2], *A. natalensis* [1,2], *A. subcoriaceus* [1] , *Cardiospermum halicacabum* [2]. *Rhus sp* [1].
8) *Charaxes xiphares penningtoni*	*Charaxinae*	*Chaetachme aristata* [1,2], *Craibia brevicaudata* [2], *Cryptocarya woodii* [1,2], *Drypetes gerrardii* [1], *Rhamnus prinoides* [1,2], *Scutia myrtina* [1,2].
9) *Charaxes zoolina zoolina*	*Charaxinae*	*Acacia brevispica* [1,2], *Adenopodia spicata* [2], *Acacia karroo* [2], *A. kraussiana* [1,2], *A. pentagona* [1,2], *A.schweinfurthi* [1,2]. *Entada abyssinica* [1,2], *E. spicata* [1,2].
10) *Bicyclus anynana*	*Satyrinae*	*Ehrharta erecta* [2].
11) *Bicyclus safitza safitza*	*Satyrinae*	*Ehrharta erecta* [2].
12) *Heteropsis perspicua perspicua*	*Satyrinae*	*Ehrharta erecta* [2], *Panicum maximum* [2] , *Pennisetum clandestinum* [2].
13) *Melanitis leda helena*	*Satyrinae*	*Cynodon sp* [2], *Ehrharta sp, Oryza sp* [2], *Pennisetum clandestinum* [2], *Saccharum officinarum* [2], *Setaria megaphylla* [2], *S. verticillata* [2].
14) *Paralethe dendrophilis indosa*	*Satyrinae*	*Ehrharta erecta* [2], *Panicum deustum*[2].

15) *Byblia anvatara acheloia*	*Byblidinae*	*Dalechampia capensis* [2], *Tragia glabrata* [2].
16) *Byblia ilithyia*	*Byblidinae*	*Dalechampia capensis* [2], *Tragia glabrata* [2].
17) *Eurytela dryope angulata*	*Byblidinae*	*Ricinus communis* [2], *Tragia glabrata* [2].
18) *Eurytela hiarbas angustata*	*Byblidinae*	*Dalechampia capensis* [2], *Tragia glabrata* [2].
19) *Sevenia boisduvali boisduvali*	*Byblidinae*	*Sapium integerrimum* [2], *S. Ellipticum* [2].
20) *Sevenia morantii morantii*	*Byblidinae*	*Excoecaria bussei* [2].
21) *Sevenia natalensis (No photo included)*	*Byblidinae*	*Sapium integerrimum* [2].
22) *Catacroptera cloanthe cloanthe*	*Nymphalinae*	*Asclepias sp* [2], *Justicia protracta* [2], *Ruellia cordata* [2].
23) *Junonia terea elgiva*	*Nymphalinae*	*Asystasia gangetica* [2], *Phaulopsis imbricata* [2], *Ruellia patula* [2].
24) *Precis tugela tugela*	*Nymphalinae*	*Plectranthus sp* [2].

25) *Cymothoe coranus coranus*	*Limenitidinae*	*Rawsonia lucida*[2].
26) *Neptis laeta*	*Limenitidinae*	*Acalypha sp*[2], *Albizia adianthifolia*[2], *Brachystegia boehmii*[2], *Dalbergia armata*[2], *D. Obovata*[2].
27) *Neptis saclava marpessa*	*Limenitidinae*	*Acalypha glabrata*[2], *Combretum bracteosum*[2], *Ricinus communis*[2].
28) *Pseudacraea luretia*	*Limenitidinae*	*Bequaertiodendron natalense*[2],*Chrysophyllum gorungosanum*[2], *C. Viridifolium*[2], *Mimusops caffra*[2], *M.obavata*[2], *M. zeyheri*[2].

a) Colour photographs of 27 butterfly species (missing no 21 S. natalensis). Sexually dimorphic species are labelled as (F-female &M-male)

1

Charaxes brutus natalensis

2

Charaxes candiope candiope

3(F)

Charaxes cithaeron cithaeron

3(M)

Charaxes cithaeron cithaeron

4
Charaxes druceanus druceanus

5(F)
Charaxes ethalion ethalion

5(M)
Charaxes ethalion ethalion

6
Charaxes jahlusa argynnides

7

Charaxes varanes varanes

8(F)

Charaxes xiphares penningtoni

8(M)

Charaxes xiphares penningtoni

9

Charaxes zoolina zoolina

10

Bicyclus anynana

11

Bicyclus safitza safitza

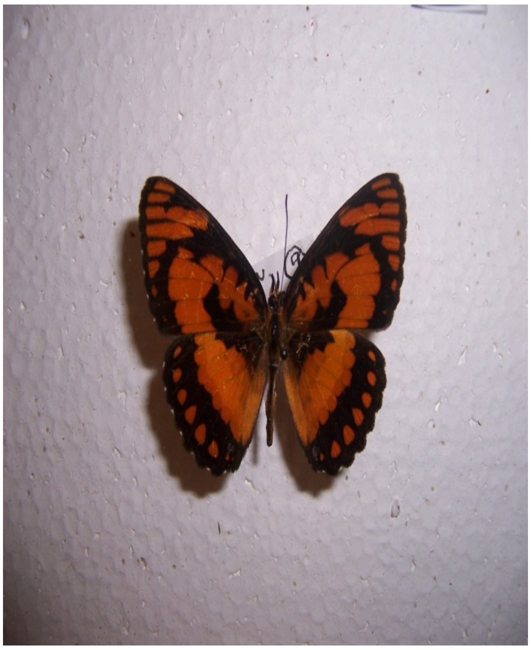
12

Heteropsis perspicua perspicua

13

Melanitis leda helena

14
Paralethe dendrophilis indosa



15
Byblia anvatara acheloia

16
Byblia ilithyia

17
Eurytela dryope angulata

18

Eurytela hiarbas angustata

19

Sevenia boisduvali boisduvali

20

Sevenia morantii morantii

22

Catacroptera cloanthe cloanthe

23

Junonia terea elgiva

24

Precis tugela tugela

25(F)

Cymothoe coranus coranus

25(M)

Cymothoe coranus coranus

26
Neptis laeta

27
Neptis saclava marpessa

28
Pseudacraea luretia