**DUNG BEETLES**

**Nichols, et al. 2008. Ecological functions and ecosystem services provided by *Scarabaeinae* dung beetles. *Biological Conservation* 141: 1461-1474**

Clear understanding of the links between ecological functions and biodiversity is needed to assess and predict the true environmental consequences of human activities

Through manipulating feces during the feeding process, dung beetles instigate a series of ecosystem functions ranging from secondary seed dispersal to nutrient cycling and parasite suppression

Many of these ecological functions provide valuable ecosystem services such as biological pest control and soil fertilization

well characterized relationships between biodiversity and ecosystem function are key to predicting the ecological and economic impacts of human activities (Armsworth et al., 2007).

Use the more fibrous material to brood their larvae (Halffter and Edmonds, 1982; Halffter and Matthews, 1966).

Ecological linkages between dung beetles and mammals have played an important role in shaping the evolution of the Scarabaeinae and the structure of extant

dung beetle communities for at least the last 40 million years (Cambefort, 1991).

The amount of dung buried by a beetle species is primarily related to mean female body size (Horgan, 2001),

these ecosystem functions often provide important and/or economically beneficial ecosystem services (De Groot et al., 2002).

The transfer of freshly deposited waste below the soil surface by tunneler and roller dung beetle species physically relocates nutrient rich organic material and instigates micro-organismal and chemical changes in the upper soil layers.

By burying dung under the soil surface, dung beetles prevent the loss of N through ammonia (NH3) volatilization (Gillard, 1967), and enhance soil fertility

This mineralization processes declines or ceases within 5–7 days, yet continues to increase in beetle-colonized dung and brood balls

a full accounting of the influence of dung beetles on nitrogen flows and distributions has yet to be done.

Several authors have reported an increase in soil nutrients (P, K, N, Ca and Mg) found in soils exposed to dung beetle activity in experimental dung masses (Bertone, 2004; Galbiati et al., 1995; Lastro, 2006; Yamada et al., 2007).

Our understanding of dung beetles’ role in soil fertility comes exclusively from pasture and grassland studies, (poor in other ecosystems) - Further research is needed in tropical forests, where dung beetles are typically capable of transferring all deposited mammal feces into the soil within hours after deposition (Arrow, 1931; Slade et al., 2007),

Tunneler dung beetles play a role in bioturbation through moving large quantities of earth to the soil surface during nesting (Mittal, 1993).

While particular nesting styles vary greatly among tunneler species, most construct underground tunnels with branching brood chambers. These tunnels can be up to several meters deep, and are often lightly backfilled with soil to protect the developing larvae

ONLY a single study has measured the impact of dung beetles on soil permeability beneath dung pats, and reported that of three species (Copris ochus, C. tripartitus and Onthophagus lenzii), only the largest-bodied species (C. ochus) had a significant positive effect on permeability (Bang et al., 2005).

A series of experimental studies link dung beetles’ role in bioturbation and nutrient mobilization to increases in plant biomass.

Studies have reported that dung mixing actions by dung beetles result in significant increases in plant height (Galbiati et al., 1995; Kabir et al., 1985), above-ground biomass (Bang et al., 2005; Lastro, 2006), grain production (Kabir et al., 1985), protein levels (Macqueen and Beirne, 1975a) and nitrogen content (Bang et al., 2005). Galbiati et al. (1995)

Borghesio (1999) found that dung beetle mixing significantly increased net primary productivity (NPP) of heathland plants in Italy over dung without beetle activity, or dung-free controls – ONLY IN SITU STUDY

Miranda et al. (2000) found dung beetle activity outperformed chemical fertilizer application in increasing plant height and leaf production at an application

Secondary seed dispersal is believed to play an important role in plant recruitment through interactions with these post-primary dispersal risk factors (Chambers and MacMahon, 1994).

with competition for dung usually intense and burial occurring rapidly, dung beetles often bury seeds, perhaps accidentally, as they bury dung

for their larval brood balls – however in some systems maybe with less competition then beetles have been known to remove seeds from the dung

Dung beetle communities bury between 6 and 95% of the seeds excreted in any given fecal pile - so basically any amount

Both the amount and origin of dung deposits affect the composition of the attracted dung beetle assemblage, but not the probability or distance of horizontal seed burial (Andresen, 2001, 2002; Ponce-Santizo et al., 2006)

Maximal recorded distances of dung beetle brood balls (presumably containing seeds) up to 15m in the Afrotropics (Heymons and von Lengerken, 1929 cited in Halffter and Matthews, 1966)

The importance of dung beetle secondary seed dispersal outside of the Neotropics (and Afrotropics to a lesser extent) is poorly known

Through feeding and nesting, adult and larval dung beetle activity serves to control the abundance of dung-breeding hematophagic and detrivorous flies and dung-dispersed nematodes and protozoa.

Bryan (1976) reported that control pats with no dung beetles contained 50 times more helminth larvae than those with 10 or 30 D. gazella pairs

Fincher reported that calves grazed on pastures without dung beetles acquired nine times more endoparasites (Ostertagia and Cooperia) than those in pastures with experimentally elevated levels dung beetles

we know of no publication empirically relating dung beetles and human endoparasite transmission

Several studies have alternatively suggested that dung beetles may transmit dung-borne pathogens within their gut or upon their exoskeleton, acting as intermediate, incidental or paratenic hosts. However few studies present convincing evidence of the role of dung beetles in transmission

When and where dung beetles and dung flies co-occur, fly survival tends to decline as a consequence of asymmetrical competition for dung resources, mechanical damage of eggs by beetles, and fly predation by mites phoretic on dung beetles. - Fly infestations reduce livestock productivity (Haufe, 1987) and hide quality (Guglielmone et al., 1999), and represent an enormous financial burden to livestock producers (Byford et al., 1992).

Experimental simulations of field conditions typically report a strong reduction in fly abundance by dung beetles in individual dung pats (Hughes et al., 1978; Ridsdill-Smith and Hayles, 1990), yet attempts to link the activity of a single dung beetle species to demonstrable reductions of natural fly populations have been unsuccessful to date

Some dung beetle species have additional unique ecological roles in trophic regulation and pollination e.g. effects on control of leaf cutter ants

some species of dung beetle are also pollinators of a couple species of plants – generally rare but very tight associations

The few studies evaluating dung beetle ecosystem services have predominantly outlined their value to the livestock industry, particularly in the context of the Australian Dung Beetle Project. – WHAT ABOUT THE TROPICS AND FOR NATURAL SYSTEMS

Losey and Vaughan (2006) estimate the net value of dung beetles to the extensively pastured beef cattle industry in the United States at USD $380 million yr-1

before dung beetle services can be properly integrated with conservation planning or practice, additional research on dung beetle biodiversity ecosystem

function (BEF) relationships and links between ecosystem functions and services will be required.

Multiple lines of evidence from temperate and tropical systems indicate that local and regional-scale changes in landuse and mammal faunas can severely alter patterns of dung beetle species diversity and abundance

Globally, tropical forest loss, modification and fragmentation are driving high rates of local extinction across forest-restricted dung beetle communities (Nichols et al., 2007),

even comparatively low annual rates of deforestation (1.4–2.0%) in Madagascar have resulted in the apparent extinction of 43% endemic forest-dwelling species

in the tribe Helictopleurini (Coprinae) (Hanski et al., 2007).

**Nummelin, M. and Hanski, I. 1989. Dung beetles of the Kibale Forest, Uganda; comparison between virgin and managed forests. *Journal of Tropical Ecology* 5: 349-352**

It is commonly believed that the vast majority of insect species living in tropical forests do not survive in areas that have been clear-cut.

Tropical forest dung beetles exemplify this phenomenon (South America - Howden & Nealis 1975, Africa - Cambefort 1984, South-East Asia - Hanski unpubl.), presumably because of the radical change in microclimate that occurs when forest is cleared (Howden & Nealis 1975).

The Kibale Forest is a medium-altitude moist evergreen forest in western Uganda (0° 27' N, 30° 26' E, 1500 m altitude). The forest area is about 550 km2, and is isolated by about 50 km from other forest areas (Struhsaker 1975).

The annual rainfall is about 1500 mm with two rainy seasons from late August to early December and from early March to early May.

We trapped beetles with human dung-baited pitfalls in March-May and September-November in 1984-86, closely following the trapping procedure described in Hanski (1983).

The virgin Kibale forest has been classified as a *Parinari* forest due to the prevalence of this conspicuous emergent tree.

Virgin forest had slightly higher species richness than selectively felled forest, while the latter had significantly higher species richness than plantations (Table 1). There are no abundant species restricted to only one forest type, though *Onthophagus cf. possoi* appears to be absent or rare in plantations.

Overall, species richness is not very high in these samples (Compared to other areas in Borneo and columbia). The rarefied species richness in a pooled sample of 453 individuals is 19.0 ± 1.8.

The relatively small size and isolation of the Kibale Forest probably explain much of this difference.

Finding do not represent the full diversity of dung beetles in Kibale forest national park

30 different species found in these traps, plus 5-10 from other trapping types and other sthat may not be trapped with this dung type. NB it should also be noted that the species keys for many of these species have never been fully worked out with many more to be discovered so this list may contain many species decribed as one.

**Lumaret, J.P., Kadiri, N. and Bertrand, M. 1992. Changes in Resources: Consequences for the Dynamics of Dung Beetle Communities. *Journal of Applied Ecology* 29(2): 349-356**

the role of dung beetles is predominant in mediterranean climates (Merritt & Anderson 1977; Lumaret & Kirk 1987),

resource. T here main guilds can be distinguished: the rollers, the tunnellers and the endocoprophagous beetles or dwellers ( according to the terminology of Hanski & Cambefort1 991).

Valiela (1974), who concluded t hat competition for food is not very important among dung-feeders in northern Europe.

Conversely,u nderw armerc limates,c ompetitionf or food appears to be stronger - In Kenya, Heinrich& Bartholomew( 1979) observedc ompetitionb etween endocoprids and rollers, and also within the ball-rollingg uild.

he amount of dung buried by tunnellersa nd rollers under laboratoryc onditionsd epends on the popu-lation density of adult beetles (Breymeyer 1974; MacQueen & Beirne 1975; Ridsdill-Smith, Hall & Craig 1982; Kirk 1983).

The variationso f overall activityo f beetles were seasonal and depended on temperaturea nd pre-cipitation

The structureo f each guild differeds ignificantly between the two sites (X2-test, PK0.001) (

DiversityH ' decreasedw hens heep faeces were replaced by cow pats, due to population in-creases of a few species

Increasesi n numbersa nd biomassw eren otu niform and re-adjustmentso ccurred both between and within guild

In dung beetle communities, the main selective factorsc ontrollingb eetle associationsa re the nature of the substratuman d physiognomic differences be-tweenh abitats( Nealis 1977; Lumaret1 983; Lumaret & Kirk 1987).

Conversely,f ood does not appear to be an important determinantin the local distribution form osts pecies (Nealis 1977).

mosts pecies use a wide varietyo f faecal matter( Lumaret 1978; Kirk& Ridsdill-Smith1 986).

The present study showed that the numbers and biomasso fb eetless tronglyd ependedo n theq uantity of the trophicr esources

**Finn, J.A. and Gittings, T. 2003. A review of competition in north temperate dung beetle communities. *Ecological Entomology* 28: 1-13**

There is little doubt that competition may be an important structuring force (Connell 1983; Schoener 1983; Giller 1984), but the widespread generality of this role has been questioned (e.g. Strong et al. 1984; Dunson and Travis 1991).

Dung beetle communities should provide a very useful study system for investigations of competiton

The dung pat comprises a delimited resurce supply that is well defined in spatial and temporal extent, easily replicated and facilitates experimental manipulation.

Akthoigh studies of comeptiton in dung beetle communities may not be common, there is no shortage of papers that invoke competiton as a prominent process in these communities.

This might be appropriate for tropical and semi-tropical dung beetle communities with hgher levels of inter and intra competition

It is not uncommon to see papers dealing with temperate dung beetles that refer to and invoke processes that are prominent and wel studied in tropical systems without the necessary equivalent in temperate areas

Dung betles come from the families *Scarabaeidae* and *Geotrupidae* with most from the scarabs and this increases towards the tropics

Combinations of small pat size and beetle abundances in previous studies resulted in very high densities and probably elicited the most extreme competitive interactions

Competiton may occer at densities considerably lower than those proposed by Landin (1961)

Holter (1975) calculated that only a small fraction (~5%) of the intialy available energy in a dung pat were assilimated by larval stages – seems unlikely since so much more of the dung is used – volume more interesting and calorific amounts of dung as this will always be low

Compettion may be very intense between larvae of dwellers that live in the dung – based on area need to live in (Holter 1979a)

Space is likely to be a limited resource for both adults and larvae in small dung pats and at times for larvae in large dung pats – this be for dwellers and makes no mention of the dung removed by indiviuals and sibling comeption within brood balls

Only 1 example of a comprehensive study on interspecific competition in northern temperate dung beetles – work carried out by Hirschberger et al. (1998, 1996, 1999). They demonstrated differing oviposition behaviour of *A, ater* in respose to high and low densities of *S. stercoraria* larvae.

Other potential example by (Yasuda 1978, 1990) but in between tropical and temperate

Some circumstantial evidence that asymmetri competition with earthworms may occur

Individual dung pats appear to provide limited opportunities for resource partitioning.

inverse relationship between no. of eggs laid and the proportion that survive to adult hood, - reasonable evidence that completion occurs between larvae – may have lead to the evolution of rollers and tuneleres who remove parts of the dung and thereby safeguard resources for their larvae

is competition is a common feateure od dung beetle communities, co-existing species would be expected to exhibit features that reduce the effects of competiton, 2 types: (1) Niche dyanamics (2) Spatial patterens of co-occurance.

Season sems an important factor in niche partitioning for dung beetles

Some studies attempting to look at interspecific competition have obvious methodlogical flaws

Spatial patterns have been considered to play an important role in dung beetle community dynamics (e.g. Hanski 1986, 1991).

Important factors for immigration to dung pats: weather, pat age, pat size, dung quality, pop abundance, species composition, mammal movements and stocking density.

These abiotic factors may set the scene for other fators such as biological interactions

Various studies have shown that independent, aggregated distributions can promote co-existance amoung potential competitor species ion ephermal resource patches (e.g. Shorrocks et al. 1979; Hanski 1987; Ives 1988).

The aggregation model of co-existance states that the aggregated and independent distribution of speices amoung resource patches may increase intra-competion with inter-specific competition, thereby facilitating the co-existance of species.

Holter (1982) found that co-occuring species tended to have positive associations between dung pats.

Tokeshi (1998) pointed out that if independent interspecific aggregation is caused by variation in patch quality, ‘aggregation become s an ephiphenomeon of resource partitioning and there is hardly a need to advocate the model as a separate mechanism of species coexistence

In addition to the role of different macrohabitat types, the diversity and types of herbivore dung (even within a single macrohabiata type) may represent another dimesion along which dung beetles may differentiate the landscape into patches of varying suitability.

According to Holt (1997) the frequency and distribution of different habiata types may influence the compostion of local assembalges.

Aggragation and metapop dynamics provide a mechanism for promoting co-existance or affecting local species composition.

Interactions amoung species may have a strong influence on the habitat suitability of a patch and the colonisation and exitinction rates of species

Competiton for space is more likely to occur thanm completion for food – amoung adults at keast but they remove space for food!!

Evidence for competition is limited – maybe between species

The effects of comeption on community structure are poorly understood – requires experimental validation

Dung lasts for much longer in temperate systems than tropical ones – raises the possibility of inter and intra specific competition in tropical systems

Priorities for future research: adopt an experimental approach, conduct experiemnts to investigate factors of dung beetles that are merely summised, use functional group approach, involve abiotic factors.

**Slade, E.M., Mann, D.J., Villanueva, J.F. and Lewis, O.T. 2007. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. *Journal of Animal Ecology* 76: 1094–1104**

There is increasing interest in the consequences that such changes may have for the important ecosystem functions provided by biodiversity

(Loreau *et al*. 2001; Naeem & Wright 2003).

under the ‘complementarity effect’, species complement each other through processes such as resource partitioning and facilitation, leading to a more efficient acquisition of resources. - Alternatively, under the ‘selection effect’, changes in functioning are suggested to result from species with particular traits being favoured and therefore dominating the mixture.

It is recognized increasingly that the abundance and traits of component species will be as important as, or more important than, species richness (Loreau *et al*. 2001; Smith & Knapp 2003; Dangles & Malmqvist 2004; Hooper *et al*. 2005)

human impacts that cause changes in functional group richness and composition are predicted to have large impacts on ecosystem processes.

Rates of dung removal and seed dispersal can be measured easily in the field, and dung beetles are separated readily into distinct functional groups based on method of dung exploitation, size and diel activity (Doube 1990; Vulinec 2002; Feer & Pincebourde 2005).

dung provides a model system for studying diversity–ecosystem function relationships because quantitative measures of resource use can be made, and because dung occurs as spatially and temporally delimited patches which can be replicated, manipulated and sampled easily (Finn 2001).

Study was carried out in Borneo

the endocoprids (dwellers) and kleptocoprids (dung kleptoparasites), were not considered in our study as they have minimal effects on dung removal over the 24-h study period.

Exclosures were made using wire mesh of two different mesh sizes (1 mm2 and 1 cm2), and a finenylon netting (0·5 mm2).

As in previous studies, rollers prevented from rolling their dung ball away would abandon it; such dung balls are rarely buried, unless beetles are concealed under leaf litter or other debris (Peck & Forsyth 1982).

The action of tunnellers was manipulated using 60x60 cm squares of either nylon mesh (to prevent dung removal by all tunnellers) or 1 cm2 wire mesh (to prevent dung removal by large tunnellers) pegged into the ground.

The experiment followed a randomized complete block design, with 10 blocks spaced by 100 m to prevent interference (Larsen & Forsyth 2005), and each treatment replicated once (positioned at random) in each block.

Each replicate used a 620 g pile of cattle dung (approximately 15 cm in diameter and 6 cm high).

Coprophagic tropical forest dung beetles tend not to specialize on particular dung sources (Hanski & Cambefort 1991)

The effects of excluding different functional groups on the proportion of dung removed were tested using linear mixed effects models, with block as a random effect.

If dung and seed removal is complementary, functional group mixtures will remove more dung or seeds than single functional group treatments. This is described as overyielding. Conversely, if one group is dominant, this group alone (and all mixtures containing it) should remove the most dung or seeds.

Excluding small beetles had a negligible effect on dung removal

removing size as a variable did not have any affect on the models explanatory power - Thus, in all subsequent analyses we used models including functional groups classified in terms of diel activity and method of dung removal, but not size.

Overall, assemblages with lower functional group richness achieved lower dung and seed removal. However, there appear to be differences among treatments having the same number of functional groups.

Overall, dung and seed removal increased with functional group richness, but the composition of functional groups present was equally important.

Complementarity exists between certain functional groups, meaning that a full complement of functional groups is required to maximize ecosystem functioning.

The most important functional group in maintaining the ecosystem functions of dung and seed removal are the tunnellers

interference or competition among dung beetle functional groups is not reducing rates of dung removal.

breaking down the dung or spreading it out, facilitating more efficient removal by nocturnal beetles.

complementarity between diurnal and nocturnal beetles appears to be more important than between tunnellers and rollers.

If species are lost from disturbed or fragmented forests, or if the relative abundance of persisting species is altered, this could have major implications for the delivery of associated ecosystem functions (Davis *et al*. 2001; Scheffler 2005; Shahabuddin *et al*. 2005).

While it may appear that within a functional group species are redundant, the responses of the species within that group to environmental change may differ (Hooper *et al*. 2002; Larsen *et al*. 2005).

Loss of the large nocturnal tunnellers, primarily *C. dayacus*, has the potential to reduce dung removal and secondary seed dispersal by around 75%.

**Vernes, K., Pope, L.C., Hill, C.J. and Bärlocher, F. 2005. Seasonality, Dung Specificity and Competition in Dung Beetle Assemblages in the Australian Wet Tropics, North-Eastern Australia. *Journal of Tropical Ecology* 21(1): 1-8**

Hill (199 6) demonstrated that beetles in rain forest and adjacent open forest had strong habitat preferences, with assemblages changing over very short distances.

Both Hill (1993) and Wright (199 7) demonstrated that most species are found only in the wetter months.

She demonstrated that significantly more dung beetle species were attracted to the dung of the rufous bettong (Aepyprymnusr ufescens) compared with the dung of Sharman's rock wallaby (Petrogale sharmani), suggesting that there is a degree of specificity for different types of mammal dung – could occur in Africa too

there was no influence of grid size on faunal diversity and abundance that we could detect.

Of the 149 collections made of dung beetles beneath trapped mammals, 13 7 (92%) contained a single species, 10 (7%) comprised two species, and two collections (1%) were made of three species

We collected 489 beetles from the three most commonly captured mammals at an overall rate of 0. 51 beetles per mammal capture. – is the number of dung beetles usually this low in Australia or is it that the methodology was poor given that this seems a kind of side look after the original study on mammals or just that the dung sizes were small or infrequent

Total numbers of beetles collected beneath traps were strongly related to a 1-mo lag in monthly mean minimum temperature (r2 = 0.91; P = 0.0002), with weaker relationships detected between beetle numbers and a 2-mo lag in monthly mean maximum temperature (r2 = 0.62; P = 0.02) and a 1-mo lag in total monthly rainfall (r2 = 0.51; P = 0.04).

fewer individuals collected per beetle species in the early wet season, and significantly more individuals collected per beetle species (principally C. subaenea) in the late wet season

Most species displayed strong habitat associations with either the Eucalyptus woodland (six species) or the Allocasuarina forest (four species;

Most studies of dung beetle seasonality suggest that activity is greatest during moist and minimal during dry periods (Doube et al. 1991).

Competiton between dung beetles for patchy, ephermel dunf resources is intense (Doube et al. 1988, Trumbo 1994) and coarse habiatat partitioning may be one way for beetles to avoid competiton.

The frequency of co-occurance of species on individual islands (or resource patches) may be regulated by competition at a finer scale (Diamond 1975).

**Sole, C.L. and Scholtz, C.H. 2010. Did dung beetles arise in Africa? A phylogenetic hypothesis based on five gene regions. *Molecular Phylogenetics and Evolution* 56: 631–641**

Although dung beetles represent a relatively small group of insects and appear to live similar lives in an apparently homogenous environment, they have a set of very complex morphological, ecological and behavioural attributes (Hanski and Cambefort, 1991) and their importance in ecosystem services has been shown to be profound (Nichols et al., 2008).

attempts at reconstructing phylogenetic hypotheses amongst large numbers of taxa are recent – lots of refs therein

at a global scale, although each of the tribes may be polyphyletic (Philips et al., 2004; Monaghan et al., 2007), studies indicate that the African lineages of the tribes are monophyletic

Speciation on the African continent has continued up to the present, resulting in the richest fauna of any region with between 40% and 50% of the world’s extant genera (\_250) and species (\_5000) (Davis et al., 2008).

All of the morphologically described genera, except Hammondantus and Heliocopris, are well supported, with a posterior probability value of 1.00 and 100% bootstrap support, and are monophyletic.

Our results indicated that the shared origin of the Scarabaeinae/Aphodiinae lineage was around 56.5 MYA although the confidence levels are weak

Our analyses show that the African tribes of rolling Canthonini and tunnelling Dichotomiini as constituted are polyphyletic

Fungus-feeding was proposed by Cambefort (1991b) and Scholtz andChown(1995) to have been the ancestral feeding pattern of dung beetles, which they hypothesised fed on detritus

obviously dispersed from a probable African origin to all the major continents and islands (Davis et al., 2002; Emlen et al., 2005).

Most of the Canthonini and Dichotomiini genera appear to be represented in Africa by relicts of a once wide-spread fauna (Davis et al., 2008).

There is well-substantiated evidence to suggest that dung beetles are actually capable of dispersing quickly and widely over considerable distances.

Complex behaviour and unusual morphology in dung beetles have been explained by a number of evolutionary theories, which include: dung translocation and burial behaviour (Halffter and Matthews, 1966; Halffter and Edmonds, 1982); differing nesting strategies (Cambefort, 1991b); sexual selection (Emlen et al., 2005); historical biogeography (Cambefort, 1991a; Davis et al.,

2002) and competition for a patchy resource (Hanski and Cambefort, 1991).

One of the compounding factors, therefore, is trying to tease apart the different taxa of ‘‘tunnellers” and ‘‘rollers” and the evolutionary history behind the behaviours

We provide strong evidence of the composition of the crown African dung beetle groups and show unequivocally that the current classification system of dividing basal dung beetle groups into a monophyletic tribe of tunnellers (Dichotomiini) and one of rollers (Canthonini) cannot be supported phylogenetically.

**Krell-Westerwalbesloh, S., Krell, F. and Linsenmair, K.E. 2004 Diel separation of Afrotropical dung beetle guilds—avoiding competition and neglecting resources (Coleoptera: Scarabaeoidea). *Journal of Natural History* 38: 2225-2249**

If a resource is an unpredictable, ephemeral patch, it is crucial for the success of any potential user to be in the right place at the right time.

Interspecific competition is inevitable on ephemeral resource patches that are used by different species in high abundance.

in humid African savannas the early occupants of a dung pat tend to use the resource more or less completely (figures 1, 2). Hence, the succession seems to follow the inhibition model (Connell and Slayter, 1977): the action of first users inhibits exploitation by later arrivals

Formation of a ball generally takes much less than 1 h, and in the small Sisyphini only a few minutes (Halffter and Matthews, 1966: 103; Doube, 1990;

The competitively superior species are, therefore, the fast telecoprids, the least competitive species are the endocoprids (Doube, 1990).

the diel activity of the species is an important parameter determining their success (Hanski, 1990)

Although temporal resource partitioning is considered to be less common compared to spatial separation and trophic specialization (Schoener, 1986), it is a widespread mechanism to avoid competition between closely related species or phylogenetically distant groups

(Krell et al., 2003), we found that guild structures of beetle assemblages in buffalo dung differ between day and night

Krell et al. (2003) found that the abundance of telecoprids and their kleptoparasites is positively correlated with the temperature of faeces and soil, whereas the number of endocoprids increases with decreasing temperature during the exposure period

Since in the savanna parkland the abundance of dung beetles is high both at night and during the day (Krell et al., 2003), we studied diel activity patterns on a site in this habitat

We deposited portions of 1 kg (900 ml) of faeces of buffalo (Syncerus caffer (Sparrman)) on the soil during 4-h periods starting 2:00 h, 6:00 h, 10:00 h, 14:00 h, 18:00 h and 22:00 h

Traps overestimate the portion of some groups containing many tourists

The abundance of scarab beetles increases strongly after heavy rainfall (Walter, 1985; personal observation). During a period of heavy rain (11–23 June) we did not expose any dung

Both the ratios of dung beetle guilds and the overall abundance of dung beetles was extremely unequally distributed over the day. The two peaks of overall abundance were at midday (48%; 829 individuals per kg dung) and around dusk (25%; 429 ind. per kg dung)

Air and soil temperatures increase between 6:00 h and 14:00 h and decrease during other times of the day. In our measuring regime, faeces have the highest temperature at 14:00 h and the lowest at 6:00 h with an average difference of 14‡C

Telecoprids and their kleptoparasites prefer the hottest time of the day (10:00–14:00 h) and are closely related to the temperature of faeces, soil and air at the end of the exposure period.

Habitat heterogeneity generally increases species diversity by enabling species that are competitively inferior in one habitat to be competitively superior in another. This heterogeneity may be spatial or temporal (Southwood, 1978; Tokeshi, 1999: 294).

Walter (1985) described a similar pattern from central Africa. Telecoprids generally prefer fresh dung without crust to make their balls. Dung pats exposed before dusk might be already too old or less attractive for telecoprids when their next activity period starts

We assume that the activity peaks of dung beetles are not correlated with the availability of dung because herbivore dung appears as an available resource all day long: buffaloes defecate randomly (Leuthold, 1977: 32), - presumably the same with elephants

From the present study also a positive correlation between temperature and the abundance of paracoprids, telecoprids and their kleptoparasites results,

The diel activity peaks of dung beetles depend on the climatic optima for the most abundant groups: the competitively superior telecoprids have their peak at midday when maximum heat enables them to perform their energetically costly rolling behaviour at the highest possible speed. The competitively intermediate paracoprids and the competitively inferior endocoprids have their peak around dusk.

**Sánchez-de-Jesús, H.A., Arroyo-Rodríguez, V., Andresen, E. and Escobar, E. 2015. Forest loss and matrix composition are the major drivers shaping dung beetle assemblages in a fragmented rainforest. *Landscape Ecology***

Degredation of forests threatens long-term persistence of biodiversity

Spatial arrangement of forest may matter as does the surrounding matrix – important factor for conservation strategies

Unclear at what scale forest loss affects biodiversity

Most studies carried out in the temperate regions – tropical studies needed

Most studies on vertabrates – broaden focus to taxa with different ecological attributes to reach more general issues – particularly for insects – impornatnt for ecosystem function (Perovié et al. 2015)

DB sensitive to environmental alterations (Nichols et al. 2007)

Many traits are known to affect DB assemblages

Human dung known to be an excellent bait – but short supply so in this study it was mixed with pig dung

Collected 9418 beetles of 43 species from 196 pitfall traps

Forest loss was best at explaining beetle assemblages, biomass and mean abundances of beetles

No. of rare species increases in larger patches

DB community composition is highly affected by matrix landuse

Larger forests contain a higher no. of forest specialists

Larger fragments also have a higher richness of mid-large mammals whose biomass has been related to increased dung beetle richness (Calot et al. 2013)

Open areas represent important areas for dispersal (Diaz et al. 2010)

DBs sensitive to forest spatial changes – therefore a good indicator of habitat modification

Deforestation and defaunafication impacts on ecosystem functions such as nutrient cycling, soil conditioning, parasite suppression and secondary seed dispersal

Conservation effort on DBs are expected to have positive effects on ecosystem functioning

**da Silva, P.G. and Hernández, M.I.M. 2014. Local and Regional Effects on Community Structure of Dung Beetles in a Mainland-Island Scenario. *PLoS ONE* 9(10): e111883**

community structure may be affected by many biotic and abiotic factors

studying local processes may not be sufficient to understanding how communities are structured

the predominance of spatial effects indicates neutral processes

DBs play a crucial role in many ecosystem services (32)

DBs are a good indicator group and are easily sampled

Community changes have potential to affect ecosystem functions performed by dung beetles – DB is an excellent model system (31)

Aim of this study: identify patterns that drive species diversity

Used baited pitfalls (again) with human faeces and rotten flesh (30g)

Used pairs of traps ~50-100m apart and left for 48hrs

Collected a total of 3004 individuals from 21 species

No. of individuals depended on the region taken from

Some species found only in some areas – spatial specialization

~10% of the variation in composition was explained by environmental effects (weather, altitude, slope)

Environmental heterogeneity had greater importance at local scales

DB composition associated with altitude - kept the dame in our study

Many DB have relationships with certain habitat characteristics - habitat specialists

**Davis, A.J., Holloway, J.D., Huijbregts, H., Krikken, J., Kirk-Spriggs, A.H. and Sutton, S.L. 2001. Dung beetles as indicators of change in the forests of northern Borneo. *Journal of Applied Ecology* 38: 593–616**

There is currently much speculation about the consequences of human-generated disturbance on tropical rainforest biodiversity, particularly impacts on species composition (Whitmore & Sayer 1992; Laurance & Bierregaard 1997) and the possibility of irreversible changes in tropical forests following logging (Reid & Miller 1989; Reid 1992).

Undisturbed lowland dipterocarp forest is becoming particularly scarce, and rapidly being diminished by logging (Marsh & Greer 1992).

The distribution of animals in tropical rainforests has also long been linked with environmental factors (Allee 1926; Janzen & Schoener 1968), and predictable environmental gradients in the forest landscape

there is still a great ignorance of pattern in tropical forest insect communities,

whole community surveys often succumb to the problem (Robinson *et al*. 1992), where inferences about overall effects of disturbance are difficult to make (see arguments by Crome 1997). To counter these problems, specific groups of organisms (indicators) can be singled out for special attention, and examined in detail (Pearson 1994; McGeoch 1998).

The local distribution of dung beetles is strongly influenced by vegetation cover and soil type (Nealis 1977; Doube 1983; Janzen 1983), and the physical structure of the forest appears to be an important determining factor in the composition and distribution of dung beetle assemblages (Davis & Sutton 1998).

Consequently, dung beetles are a useful indicator group because they reflect structural differences (i.e. architectural, abiotic) between biotope types;

The rationale for using dung beetles as indicators of disturbance has been reviewed by Halffter & Favila (1993).

Used baited pitfall traps and flight interception traps

Pitfalls in the main collecting programme were baited with human faeces: a proven attractant to dung beetles in rainforests, which attracts a wide spectrum of species

The material analysed here represents 86 species from 35 279 identified specimens

These results suggest that FIT give a more comprehensive sample of the beetle species present in a given area.

Both pitfall and FIT data showed clustering of species into several distinct associations, each association having a distinct ecological character or shared habitat.

Data showed that species richness in logged forest was generally higher than individual transects from primary interior-forest, closer to species richness in riverine forest

Disturbance does not increase species richness *per se*, but species distributed along environmental gradients in primary are mixed at the same spatial location in logged and plantation forest (Davis & Sutton 1998; Davis, Huijbregts & Krikken 2000).

Species assemblages in disturbed biotopes are therefore ‘composite’, in that the whole assemblage contains a mixture of species associations from different biotopes that tend to be spatially separate in interior-primary forest.

The data show decreased dung beetle diversity in logged and plantation forest,

Results presented in this paper suggest that dung beetle assemblages in selectively logged forest following traditional practices closely resemble riverine rather than interior-forest assemblages

Moderate human disturbance, which leaves a relatively high tree species diversity, has been shown to have surprisingly little, if any, effect on insect diversity (Wolda 1987). – as in Kibale

Data presented here show that species distribution patterns for individual associations within discrete biotopes respond to disturbance,

**Nummelin, M. 1990. Relative habitat use ·of duikers, bush pigs, and elephants in virgin and selectively logged areas of the Kibale Forest, Uganda. *Tropical Zoology* 3: 111-120**

The number of elephants in the Kibale Forest is roughly 1/5 of that recorded 20 years earlier. Elephants preferred selectively felled areas. – study from 1983-1984 so elepant number measured from mid 60s

Even on a world scale the ecology of tropical forests is poorly understood with regard to forestry practices MYERS 1984). – may have improved since then due to studies including those of Ewers and co.

The Kibale Forest is a medium altitude moist evergreen forest in western Uganda (0°13' to 0°41'N and 30°19' to 30°32'E). Average elevation is ca 1500 m a.s.l., and the yearly rainfall is roughly 1500 mm (Fig. 2). Kibale differs from lowland tropical rainforest in having higher altitude, lower temperature, and lower rainfall, but otherwise it possesses most of the typical features of lowland forests (LANGDALEBROWN et al. 1964).

Each study habitat (all of them over 1 km2 in size) had 50 X 50 m trail grid system. The trails are ca 1 m wide (total length over 200 km), and kept walkable by Kibale Forest Project personnel. All studied habitats were connected to each other by natural forest.

*Kl5, selectively felled* In this study area the forest was selectively felled in 1968-1969. Total harvestaveraged 21 m3/ha (SKORUPA & KASENENE 1984). The area was heavily disturbed bythe felling

Both elephant and duiker dungs occasionally persists on the ground for more than a month.

The number of Diker pellet piles found correlated negatively with the rainfall of the previous month.

There was a weak (but non-significant) positive correlation with the rainfall of the previous month in the numbers of bush pig diggings found

The number of elephants has decreased drastically since the last census during the early sixties (WING & Buss 1970). The estimated number of elephants on the basis of dung heaps recorded in the present study is 200 individuals,

density estimates of 4.1 elephant dung heaps per hectare in K30, 0.4 heaps/ha in virgin Ngogo, 3.1 heaps/ha in logged K14, 25.9 heaps/ha in logged K15.

methods of estimating the population densities of extremely shy duikers and bush pigs in Kibale are very hard to conduct (GHIGUERI et al. 1982, see also KosTER & HART 1988).

The reliability of dung counts for analyzing the relative population densities of elephants has been criticized (e.g. ]ACHMANN & BELL 1984).

elephants are shown to favour secondary forest to the natural forest (SHORT 1983, MERZ 1986). But also the poaching of the elephants in the Kibale Forest may affect the habitat choice of the animals.

**Krell, F., Krell-Westerwalbesloh, S., Weiß, I., Eggleton, P. and Linsenmair, K.E. 2003.** **Spatial separation of Afrotropical dung beetle guilds: a trade-off** **between competitive superiority and energetic constraints** **(Coleoptera: Scarabaeidae). *Ecography* 26: 210–222**

Formation of a ball generally takes much less than one hour, in small Sisyphini only a few minutes (Halffter and Matthews 1966

Full tunnel construction is relatively time-consuming and takes at least six hours (Doube 1990).

The competitively superior species are therefore the fast telecoprids, the least competitive species are the endocoprids (Doube 1990

Success of any species in occupying any vacancy in the biocenosis is determined mostly by its early presence or arrival, especially if species are able to monopolize a part or the resource – ‘‘first come first served’’ (e.g. Tokeshi 1999

The objective of the present study was to find out if competitively inferior dung beetle guilds use the habitat heterogeneity to coexist locally with superior competitors.

A matrix of different savanna types contains discrete patches of forest habitats with abrupt borders, such as gallery forests and forest islands – also seen to an extent in western Uganda

dung beetles can fly up to ~1 km to forage (Paik 1976: 167, Hanski 1980, Roslin 2000),

we deposited 20 portions of 1 kg (900 ml) fresh faeces of buffalo (*Syncerus caffer* (Sparrman), Bovidae) on the soil in each of the three habitats.

For our experiments we used fresh dung since, in the study area, old buffalo dung is virtually absent in the savanna during the first half of the rainy season.

Barth et al. (1994) showed that the coprocenoses of artificially formed and naturally voided dung pats do not differ significantly

Since in natural tropical habitats the first dung beetles arrive at the dung less than one minute after deposition, it is impossible to find uncolonised fresh dung.

In the open habitats (savanna and river valley), the absolute number of dung beetles is ca 10 times higher than in the dense gallery forest

In the gallery forest paracoprids make up a large portion of the dung beetlefauna, in the savanna telecoprids and paracoprids.

In the gallery forest, the abundance of dung beetles in buffalo dung is low (22\_8 individuals/kg dung; at night 66\_38 ind. kg−1 dung). They certainly occur at a non-competitive level.

The change of the air temperature during the experimental period of 10 h during the day is significantly higher in the open habitats than in the forest. In summary, the temperature changes of the soil and faeces are much greater in the open habitats than in the forest.

In different adjacent habitats abundance and guild structure of dung beetle assemblages clearly differ

the savanna is the habitat where spatial separation in the competitively inferior guilds may serve as a competition avoiding strategy.

environmental diversity may not only increase the number of species but also the number of functional types (guilds) in an area

The area size of a habitat type does not necessarily determine the abundance of dung beetles, but the structure of vegetation does

Elephants produce coarse dung and duikers piles of small pellets, whereas buffalo faeces have a fine and homogenous texture – but generalist coprophages could use all these types of dung.

Bartholomew and Heinrich (1978) found that the velocity of beetles increases with the body temperature, which in some species can be increased endothermically.

The statement that endocropids ‘‘usually play an insignificant role’’ in Afrotropical coprocenoses (Cambefort 1984: 17, 1991: 161) has to be revised.

**Giller, P.S. and Doube, B.M. 1989. Experimental Analysis of Inter- and Intraspecific Competition in Dung Beetle Communities. *Journal of Animal Ecology* 58: 129-142**

Ephemeral resources such as dung pads offer discrete patches of non-renewable resources to a well-defined and diverse fauna

In hot moist seasons in tropical and subtropical regions, large numbers of species and individuals and rapid removal of entire pads strongly suggest that resources can be limiting and that competition can be intense (Anderson and Coe 1974; Kingston 1977; Heinrich and Bartholomew 1979; Peck and Forsyth 1982; Hanski 1983; Janzen 1983)

Dung is a realtively homogenous resource and therefore presents beetles with little opportunity for specialization within a single resource patch

One might except a priori that competition would be a major determinant of community organization in such systems

An evaluation of the role of competition in structuring dung beetle assembalges and in the wider context of community organization however, requires a systematic experimental analysis of the competitive process.

Dung beetles are well suited for studies on competition: rich fauna of community; microhabitat is limited; distinct guilds of DB; easy to manipulate

Dung communities also resemble a number of other communities with similar general characteristics

There are over 2000 species of dung beetle in sub-shararan Africa

They looked at two species of telecropid (tunnellers) which differed in burial rate – then looking at the intra and inter specific competition

Each pad used in this experiemt weighed kg – how much is this in volume? 1.5l? 1l?

They also used volume to measure the quantity of dung remaining which seems to be a better method than the mass of the dung

There seemed no affect of moisture on the amount of dung buried between the different treatments

The absence of other species, increasing the density of *O.alxis* increased the amount of dung buried but decreased the amount buried per pair

However the presence/absence of *O. alexis* had no effect on the burial amount of the other coprine species

The amount of dung per species can only be measured I single spoecies treatments and not in competition

Competition for dung amoungst DBs can be translated directly into reduced reproduction at the single pad level, as seceral studies have documented a negative correlation between beetle density and brood mass production (e.g. Holter 1979; Ridsdill-Smith et al. 1982)

Lab and field have almost the same results

In all three species, dung burial per pair clearly decreases with increasing beetle density (Figs 2, 4). Intraspecific competition was evident from between two to four pairs of 0. alexis and above two pairs of coprine beetles per 1.5 kg pad

The nature of intraspecific competition in 0. alexis is likely to be mainly exploitative, although there is the possibility of interference in tunnel construction and beetle activity rendering some of the dung unusable for brood production (e.g. Ridsdill-Smith, Hall & Craig 1982).

The presence of 0. alexis had a small effect, if any, on buried dung recovered from either coprine species in both Experiments A and B

In contrast, presence of two or three pairs of coprine beetles and above severely affected 0. alexis (Figs 1, 3). There was thus strongly asymmetric interspecific competition between coprine and Onitis beetles.

At lower beetle density (eight pairs per pad), there was little intraspecific competition in the 2 litre and 3 litre pads (producing forty-five and forty-two broods per pad), but significant competition in 1 litre pads (producing twenty-five broods per pad)

The direction of these competitive interactions and their significance on paracoprid reproduction are unknown. This is also true for another group of potential competitors, the diurnal telecoprids (ball rollers).

Experimental studies on pad colonization and co-occurrence of coprine and onitine beetles, has shown that in over 28% of all dung pads colonized after only 12 hours exposure to colonists, densities were such that competition was likely to occur

where pre-emptive competition of any resource is important, the temporal sequences of arrivals will have profound effects and influence the outcome of competitive interactions.

dung age and the colonization sequence of species will also influence the outcome of competitive interactions at the pad level

**Hanski and Camberfort 1991. *Dung Beetle Ecology***

For dung beetles, droppings are concentrations of high quality resources for which competition is severe

The resource patches are often fiercely contested and it is not surprising that DBs have evolved means of out manoeuvring each other

Three types of dung beetle: rollers, tunnellers and dwellers, (telecropids, paracropids and endocropids, respectively

Animal droppings best example of minor habitats (Elton 1949)

DB ecology is about exploitive competition

Apparent contradiction of the competitive exclusion principle – Gause’s law (1934)

Lack of experiments on competition of DBs

Microhabitats stand out of the matrix as ‘islands’ of high quality resources

DB not as specious as other groups – maybe due to limited spcialization

Interctions may occur between DBs and Microbes (Hanski 1982)

Ty[e of competition (scramble, defense) depends on the size (and temporal availibilty) of the resource

Elephant poo probs to large to be secured by one individual, so mixed communities of scramble competitors that aim to collect their share

Lottery dynamics (Sale 1977) could allow the existence of similar competitors due to fluctuating populations – could be at play in DBs, though maybe not for large relative patches such as elephant dung as these cannot be monopolised

Variance/covariance dynamics may be better (Hanski 1981)

Can’t assume that natural patches are the same – best to manipulate patches

Environmental factors (e.g. humidity, soil type) affect the coexistence of DBs

Large poo cannot be defended - many species

Rollers emerge as a result of competition for space

Most DBs are iteroparous - multiple breeding attempts

DBs are centred mainly on mammals dung – debate on if they stated on this resource or merely specilaed with the rise of mammals in the last 50my.

Species richness is lower in forests than in the savannah

Rollers are also less dominant in the forest – but they are extremely dominant in the savannah

>2000 specie are found in sub-sharraan Africa

Up to 7 functional groups identified in southern Africa – fast/slow tunnelers etc but all based on the main guild principle and maybe just subdivision just for the sake of it

Soil type is an important fator in experiements – use similar areas

Lack of relevant emipiracl studies, not lack of competition explains why beetles have not featured in reviews of the incidence of comepetition in natural populations (Connell 1983)

Competition may be the only interspecfic interaction of importance

Competition mainly from anecdotal observations both within and between spcies – this widely assumed force is poorly understood despite the huge array of ecological and evolutionary research in this area which may be over assumed and flawed in many cases

**### not sure if from book or own writing – but probs own writing for intro**

Competition is a powerful ecological pressure on individuals potentially driving altering the behaviour and ultimately driving speciation and niche differentiation to avoid the debilitating effects on fitness of competition. When resources are scare competition will be intense, therefore, measures to avoid competition will arise. However, in areas of high competition (e.g. Tropical rainforests) are also more species rich with many competitors for the same resource.

**Simmons, L.W. and Ridsdill-Smith, T.J. (2011). *Ecology and Evolution of Dung Beetles*. Wiley-Blackwell**

Page 1-2

Beetles make up ¼ of all described species, with 35,000 scarabeaoidea including dung beetles and stags (Hunt et al. 2007)

~6,000 dung beetle species in 257+ genera – excellent study system

The paucity of studies on dung beetle competition reported by Hanski and Camberfort (1991) has been addressed with respect to reproductive competition

Page 9-19

Definitions of paracropids (tunnellers), telecropids (rollers) and edocropids (dwellers) based on the way that they use dung

Current evidence suggests that tunneling is the ancestral state with several gains of telecropid state

Reproductive competition has undoubtedly played an important role in the evolutionary diversification of breeding behaviour in DBs

H and C suggest a competitive hieracy in DBs with rollers at the top and dwellers at the bottom

NICE DIAGRAM PAGE 11 OF THE DIFFERENT TYPES OF DB

Large amount of parental care especially from females which in some species is essential for the survival of the larvae – may become an ideal model system for studying the evolution of parental care

The very different environments in which dung beetles must operate will also generate different selection pressures on their morphology

Intraspecific competition is common in DBs (h and C 1991)

Large numbers of Dbs of many species can arrive at the same fresh dung pads – over 1000 beetles can be caught in a single pitfall trap in 24hrs (H and C 1991)

Most of the examples of interspecific competition are between rollers where contests can be easily seen – in genral larger species capture dung from smaller species

Competition for resources wil reduce individual fitness and generate selection on traits that reduce the intensity of competition. When 2 species exploit the same resource, those individuals within each species that compete least with members of the other species are expected to have higher fitness, generating disruptive selection and niche divergence (Slatkin 1980; Day and Young 2004)

Different species within the same region have evolved differences in diet, nesting behaviour, thermal tolerance and visual acuities to fill different niches

There is alos much variation within the guilds of dung beetles (Doube 1990)

Despite competition, it is possible for many species to coexist in a DB community and in nay one community the different species occupy many diferent niches

The high species richness of tropical communities makes an analysis of the factos influencing community structre hard to asses

A regional decline in medium to large sized animals has severely disrunpted the diversity and abundance of DBs (Nichols et al. 2009)

DBs could be used as a ecological disturbance indicator

Page21-24

DBs are one of the most morphologically diverse groups of orgnaisms with 6000 species – this is large group but not overwhelmingly so as can actually be grasped

They posses a number of characteristics that can enable one to sample their diversity realtively easily and use these data to asses the health of ecosystems (Spector 2006)

Great increaein the number of phylogenetic studies on DBs that have clarified the relationship of tribes and guilds – this shows that the evolution of DBs is not as parsimonious as previouslt thought

The sarabs are a cosmopolitan group with species found on all continents apart from south pole with the greatest diversity in sub-saharan Africa, south America

23 tribes of DB have been identified which is V confusing and lots and lots of species with o clear patterns of guild membership at least not monophyletically

Page 36-44

Many species of Db have particular patterns of day when they forage

Larger beetles are more active during the warmest part of the day and smaller ones at night

Mammal dunf represents a rich source of nutrients based in large part on the bacterial content, sometimes high in N, abundant carbs, vitamin and minerals

Most Dbs are generalists to various degrees and relatively few species have ben recorded on just one type of dung

The variety of food type does indicate flexible strategies that have evolved in order for adult to survive and reproduce under various conditions

From ancestral tunnellers, DBs known as rollers evolved the ability to construct balls of dung – presumed to avoid the tremendous competition faced for the ephermal food resource of dung

Dwellers are relatively rare form of behaviour derived from tunelleing

Kleptoparasites may compromise 10% of species in some habitats (krell et al. 2003)

Page 57

Recent phylo work indicates that tunnelling was the ancestral behaviour in DBs and that rolling behaviour has evolved multiple times independently

Seems that horns have evolved 8 times in DBs, with each occurance associated with tunnelling rather than ball rolling, maybe because of the more intense on site competition experienced by tunnelllers

Page 87-91

DBs use smell to find parches of dung – however olfactory ecology of DBs is poorly understood

Not sure which chemicals are used by the beetles to find dung – maybe why so many generalists

Able to discriminate between the dung from different herbivores

The chemicals emitted from dung piles also differ over time potentially deteriming the temporal variation of species that occur in the dung

Page 245-250

DBs have been used to provide ecosystem services and bio control especially in Australia

DB introduction programmes aim to improve nutrient cycling as well as the control of dung-breeding flies (Bornemissza 1976; Finchler 1981)

Ecosystem function provided by DBs include nutrient cycling, mixing of dung into the soil, plant growth enhancement, secondary seed dispersal, parasite control and fly control (Nichols et al. 2008)

Studies in grasslands demonstrate a strongly positive role on consumers in returning nutrients to plants including N, P and K (Loreau 1995)

At Tsavo NP during peak season a 2kg dung pat of elephant dung was removed completely by ~17,000 DBs in just 2 hours (Coe 1977)

In many ecosystems the nutrients associated with mammal dung are made available to plants primaliy through the actions of DBs (Nichols et al. 2008)

The control of dung breeding flies has been a major ecosystem service provided by DBs to the cattle industry with introductions done for this purpose in Australia and N America

DBs also control other parasites such as midges that transfer viruses and control of cattle nematodes

Page 262

DBs co-existing in fresh dung occupy many different niches and interspecific competition is likely to have played a crucial role in the evolution of niche divergence

There are few studies of interspecific competition in action

Page 267-286

There is a case for the use of the sarabidae as an ecological indicator taxon

DBs are appealing in this regard as sampling is very cost effective and can take only days rather than weeks or even months as for other taxa

Efforts to investigate quantitative effcienices of different collecting protocols is underway using ScarabNet

DBs may be great incators of environmental change due to: natural environmental gradients , land use change and intensification - especially in tropical forests, declines in resource diversity and avilibilty

* SEE THE PAGES 272-286 FOR DETAILS ON THESE AREAS

**COMMUNITY ECOLOGY**

**Ives et al. 1999. Stability and Variability in Competitive Communities. *Science* 286: 542-544**

The stability of an ecological community is thought to depend on the number of species it contains and the strengths of interactions between them (*1*).

Experimental studies (*3*) showed that large communities of plant competitors may be more stable than small communities when stability is measured in terms of the total biomass of all species.

Our analyses address the effects of interspecific competition and species diversity on variability in the biomass of individual species and variability in total community biomass.

Species interactions then act as a filter through which short-term environmental variability is translated into long-term variability in biomass

For both models, increasing the strength of competition (either intra- or interspecific) reduces biomass

Community-level variances are almost identical for both models (Fig. 2), indicating that interspecific competition has little influence on community-level variances.

Increasing the number of species *n* in most cases decreases community-level variances - This reduction in community-level variance with increasing *n* has been called “statistical averaging” (*10*) or the “portfolio effect” (*11*).

Our main result is that interspecific competition and species number have little influence on community-level variances; the variance in total community biomass depends only on how species respond to environmental fluctuations.

**Lehman, C.C. and Tilman, D. 2000. Biodiversity, Stability, and Productivity in Competitive Communities. *The American Naturalist* 156(5): 534-552**

May (1972) showed that simple models of interspecific competition became less stable—as measured by their ability to return to multispecies equilibria after perturbation—as the number of interacting species increased

McNaughton (1977) strongly objected to the rejection of the diversity-stability hypothesis based solely on theory – idea stil took hold amounst some ecologists

lots of research over the next 20 years on if diversity and stability are linked

Yachi and Loreau (1999) showed that under rather general conditions, increased species diversity should not only reduce the variability of community properties such as productivity but also increase the temporal means of those properties.

All revealed consistent effects of diversity on temporal stability: community variability decreased and population variability increased as species diversity increased

Stability has a multiplicity of meanings in ecology, both qualitative and quantitative

Because many different combinations of species may be able to coexist in a multispecies community, the temporal stability measure is taken as an average over many different communities.

when the reduced variances of individual species are summed to calculate variance in total community abundance for equation (1), the ecosystem may be temporally stabilized purely on statistical grounds. – called the portfolio effect

covariance provides a measure of species interactions, tending to be negative for competitors, positive for mutualists, and near 0 for noninteracting species.

we examine three different models of interspecific competition to determine the dependence of temporal stability on diversity - a mechanistic model, a phenomenological model, and a probabilistic model

Resource-based models of competition (e.g., Tilman 1980) can be modified to have each species’ resource dependent growth rate depend on a time-varying physical factor.

In an unchanging environment, this system would exhibit competitive exclusion. In a variable environment, however, many species may persist (fig. 1*B*). The abundance of all species constantly varies, and this variation allows coexistence (Chesson 1986, 1994).

no monocultures were as productive as some two-species combinations, no two-species combinations were as productive as some three-species combinations, and so forth

species composition, as well as diversity, was a major determinant of temporal stability, as it was in the case of productivity.

on average, diversity decreased the temporal stability of individual species yet increased the temporal stability of the entire community

In this resource model, as in nature, species that compete most strongly might be expected to have the strongest negative effects on each others’ abundances. Likewise, species with very different requirements should have a negligible effect on each other.

Even though very similar species might inhibit each other strongly, they also flourish under similar environmental conditions, and that leads to positive covariance for similar species under this kind of temporal coexistence.

Suggests that temporal stability of individual species will be sensitive to the strength of competition but temporal stability

of the entire community will not.

Diversity still temporally stabilized the community while destabilizing individual populations, but the strength of competition had little effect on the magnitude of stabilization of the community.

First, greater interspecific competition (e.g., *v* p 0.9) produces more negative covariances among species, tending to increase temporal stability of the community. Second, however, greater interspecific competition leads to less overyielding, tending to decrease the temporal stability of the community (see eq. [1]; app. A; eq. [A2]). These two effects roughly cancel

for example, the idea that the tropics are more diverse than temperate zones, in part because the tropical environment is less variable (e.g., Abrams 1976; Nisbet et al. 1978).

All three models of competition examined here predict similar qualitative dependence of temporal stability on diversity; with respect to variation in biomass, diversity stabilizes the community but destabilizes individual populations.

Diversity increases temporal stability at the community level, in agreement with Elton and other early investigators, but decreases stability at the population level, in agreement with May and later investigators.

**Tilman, D. Competition and Biodiversity in Spatially Structured Habitats. *Ecology* 75(1): 2-16**

Strong neighborhood interactions are also the rule for motile species that consume ephemeral and patchy resources (Hanski 1990, Shorrocks 1991).

However, because each individual organism exists at a discrete point in space, there are unavoidable site-to-site differences in the local biotic composition of a habitat caused by random colonization and mortality.

the discreteness of individual organisms means that all organisms live in a spatially structured, subdivided habitat.

There have been numerous theoretical demonstrations that habitat subdivision can allow two species, a fugitive species and a superior competitor, to stably coexist as metapopulations (e.g., Skellam 1951, Levins and Culver 1971, Horn and MacArthur 1972, Armstrong 1976, Hastings 1980, Shmida and Ellner 1984).

there is increasingly strong evidence that spatial subdivision is an essential factor controlling the species dynamics and biodiversity of many communities.

Explanations of diversity require an interspecific trade-off.

Could it be that superior competitors are prevented, by their poorer colonization abilities, from occupying the entire landscape, and that this provides sites in which numerous species of inferior competitors can persist?

Hanski (1990) suggested that natural diversity was maintained by interspecific differences in competition and dispersal abilities.

a species can persist in a habitat only if its colonization rate, c, is greater than its mortality rate, m.

Nee and May (1992) showed that increased habitat destruction led to increased abundance of a weedy, fugitive species in the portion of the habitat that was undisturbed.

Previously published work has clearly demonstrated that spatial subdivision may allow the stable coexistence of two species that are incapable of coexisting in any single site – this can be generalised to any number of species

There is no limit to the number of species that can coexist stably in a spatially subdivided habitat, even though the best competitor would displace all other species from a habitat that was not spatially subdivided.

Limiting similarity means that it is not sufficient for an inferior competitor to have a lower mortality rate and/ or a higher colonization rate than its next best competitor. Rather, its traits must differ from those of its superior competitor by a finite amount that depends, mainly, on the abundance of its superior competitor.

These analyses have shown that competitively adjacent species can coexist only if the colonization and/ or mortality rates of the inferior competitor are sufficiently different from those of its next best competitor.

As Pacala (1986a, b), Ives (1988), and Hanski and Cambefort (1991) have shown, neighborhood interactions and local dispersal increase intraspecific competition relative to interspecific, and thus encourage stable coexistence.

These results indicate that there need be no limit to species richness in a spatially subdivided habitat with a single limiting resource,

Hubbell and Foster (1986) hypothesized that each guild contained large numbers of functionally identical species for which

competitive displacement would not occur. Rather, the abundances of such species would be determined by random local mortality and colonization - kind of superseded by this paper

As Hubbell and Foster (1986) noted, the more similar two competitors are, the slower should be the rate of competitive displacement.

An alternative explanation for species diversity is that habitats are spatially heterogeneous, and that such heterogeneity allows coexistence (e.g., Tilman 1982).

**Palmer, T.M., Stanton, M.L. and Young, T.P. Competition and Coexistence: Exploring Mechanisms That Restrict and Maintain Diversity within Mutualist Guilds. *The American Naturalist* 162(S4): S63-S79**

How do multiple species coexist within guilds of mutualists in the face of potentially strong competition?

because members of mutualist guilds compete for a dynamic resource that may be under reciprocal selection with its partners, studies within these guilds may provide insight into novel coexistence mechanisms.

In the absence of competition, mechanisms of coexistence need not be invoked to explain species diversity within guilds.

Interspecific competition occurs when one species reduces the access of another species to a necessary resource that is in limited supply

In the absence of such data, we often assume that if the average performance (e.g., foraging rate, fertility) of individual mutualists is increased by greater access to partners, then the availability of partners represents a limiting resource

The majority of coexistence mechanisms may be codified as forms of niche partitioning within heterogeneous environments (Cody and Diamond 1975; Whittaker 1975; Chesson 1991) by allowing that niches include both spatial and temporal axes of environmental heterogeneity

Coexistence within guilds may be facilitated when species exhibit trade-offs between competition and colonization abilities. – similar to the tilman paper

A third class of coexistence models addresses systems in which recruitment limitation or aggregation minimize the effects of interspecific competition

a key question is not whether each of these mechanisms plays a role in diversity maintenance but to what extent.

Typically, competitively subordinate pollinators respond to release from competition by broadening of the spectrum of flower species they visit (Primack and Howe 1975; Inouye 1978; Bowers 1986) and/or by increasing time spent visiting high-yield flowers and patches (Morse 1982; Hingston and McQuillan 1999). – similar behaviour in dung beetles?

An alternative but underused experimental approach is to increase or decrease the amounts of floral reward available within a site and then measure changes in pollinator behavior or performance that are (or are not) consistent with competition for naturally occurring floral resources. – we kind of increased the amount avilible to other groups by excluding one

Resource partitioning among copollinators may be a widespread phenomenon that minimizes interspecific competition for floral

resources and that facilitates the persistence of pollinators that are not competitively dominant

it will be important to monitor how multiple species within the pollinating guild respond to manipulations of competitors or resources rather than considering just one or two focal species (Macnally 1983).

Because flowers are relatively immobile resources that are patchily distributed over space, patch dynamics may contribute to the persistence of competitive subordinates in multispecies pollination guilds – same can be said for dung piles

Spatial variation in resource quantity or quality may facilitate coexistence if there are interspecific trade-offs in the ability of species to exploit resourcerich versus resource-poor patches (e.g., Kotler and Brown 1988; Hanski 1989)

In relatively uniform habitats, theory suggests that competing species may coexist through intraspecific aggregation (e.g., Hanski and Cambefort 1991; Ives 1991; Bolker and Pacala 1999), which increases the intensity of intraspecific relative to interspecific competition

There will only be selection for greater partner specialization if a given mutualist is consistently the most effective mutualist over long timescales

**Davies, Krebs and West. Introduction to Behavioural Ecology**

Chapter 5 – Competing for resources page 116-145

When many individuals exploit the same limited resource they become competitors and the best way for one individual to behave depends on what its competitors are doing

ESS (Maynard Smith and Price 1973) in play for the dung beetles? Is the best strategy to avoid interspecific competition? Does it matter since the effect of intraspecific competition is so high?

May be a dove like strategy being played by the different guilds, both benefit from avoiding competition leading to resource sharing over time

As more newcomers arrive at a resource then it becomes less attractive to new comers – hence [otentailly leading to lower levels of competition in each patch – ideal free distribution (Fretwell 1972)

- unlikely in this system as beetles can take resources away and defend them

– also since all of our patches were

With resource defence the early arrivals aquire resources and prevent their use by new arrivals. This leads to all the resource in an area being used by these first individuals. This seems likely based on what we know of dung beetles who remove dung for their young.

However different guilds may not be equal comeptitors and it has been suggested that rollers may be more effective at using the dung. This would lead to a resource distribution with unequal comeptitors where each guild is best at exploiting the dung in its own way and have diverged to take advantage of this.

**Connell, J.H. (1980). Diversity and the Coevolution of Competitors, or the Ghost of Competition Past. *Oikos* 35(2): 131-138**

Interactions of various sorts confer structure on the community:

Whereas some of these interactions are positive for both members (mutualistic) or positive for one with no apparent harm to the other (commensals), those that are negative for one or both species (predation, parasitism, competition) present a problem, namely how do such antagonistic pairs of species persist together without one driving the other extinct?

If each species is a superior competitor on a different range of such environmental conditions, several competing species will be able to coexist at equilibrium.

There are two general ways in which this situation may have come about: 1) species are preadapted to different sets of conditions and then come together again, 2) species have coevolved to use different sets of conditions to avoid competition

Despite all the theoretical attention it has received, there remains a real question as to how much this notion of competition led competition applies to real communities and what sorts of circumstances would promote coevolutionary partitioning of resources between competing species.

the more interdependent two species are, the more likely it is that they will co-occur and so coevolve – DBs are super diverse and they is lots of species present in each ‘microhabitat’ so they may not actually be that interdependent (lots of intraspecific competition)

The likelihood of coevolution between two competing species depends upon how similar their resource requirements are and how often they meet

High species diversity is often associated with changing species composition, as during the inter-mediate stages of a succession after a disturbance (Connell 1978).

The combination of changing species com-position and high diversity further reduces the probability of consistent co-occurrence of a particular pair of competing species.

The upshot of this discussion is that coevolution is more likely to happen (a) in pairs of species on different trophic levels than in pairs competing on the same trophic level, (b) in communities with low species diversity in which there are low rates of change of species composition.

The surest method is a field experiment in which the distribution and abundance of one or both species is manipulated (Connell 1974, 1975, Colwell and Fuentes 1975).

if carefully controlled and replicated, field experiments offer perhaps the strongest evidence for the existence of competition in natural populations.

niche space is probably multidimensional, yet it is impossible to obtain data on all relevant dimensions (Pianka 1975).

even if the species overlap in resources they may not compete (Menge 1979).

Many details on how to demonstrate competition between species by looking at niche breath. V similar if more complicated than what we did including the use of a positive control

In diverse tropical communities, competitive interactions also appear to involve many, not few, species.

Therefore I conclude that coevolution of competitors is also un-likely in communities of high diversity.

I have proposed (Connell 1975) that interspecific com-petition is more likely to happen in moderately harsh physical environments than either in very harsh or in benign conditions.

it is more likely that they diverged as they evolved separately so that, when they later came together, they coexisted because they had already become adapted to different resources or parts of the habitat.

I will no longer be persuaded by such invoking of "the Ghost of Competition Past".

**Shorrocks, B., Rosewell, J., Edwards, K. and Atkinson, W. (1984). Interspecific competition is not a major organising force in many insect communities. *Nature* 310: 310-312**

Part of the current dogma in ecology is that competition between species for limited resources is not only common but also a major organising force in many communities (1,2)

This belief is mainly driven by work on vertebrates

Other workers, particularly those working on insects have suggested that significant interspecific competition is too rare and sporadic to be of major significance and have placed more emphasis on autecological processes (10-13)

Question of if competition is common in nature (1)

Conclusions of these people based on lots of community experiments with drosophila

Drosophila species will rarely exclude one another in nature even if they show no traditional resource partitioning and compete most strongly

The removal experiments collected by Schoener (1), although providing evidence of competition in natural communities do not necessarily imply that competition is present and is a major organising force in community structure and therefore in community function.

**Pianka, E.R. (1974). Niche Overlap and Diffuse Competition. PNAS 74(5): 2141-2145**

Current theory predicts a distinct upper limit on the permissible degree of niche overlap; moreover, theory suggests that maximal tolerable overlap should be relatively insensitive to environmental variability

within the lizard subset of natural desert communities, niche overlap decreases both with increasing environmental variability and with increasing numbers of lizard species.

All else being equal, a community with more resource sharing, or greater niche overlap, will clearly support more species than one with less niche overlap.

Population biologists have reasoned that coexisting species must differ in their ecological requirements by at least some minimal amount to avoid competitive exclusion.

However, tempting though it may be, equating overlap with competition is an extremely dubious and misleading procedure (10, 11).

If resources are not in short supply, two organisms can share them without detriment to one another.

Thus, extensive niche overlap may actually be correlated with reduced competition.

Pairs with high overlap along one dimension often overlap relatively little along another, reducing overall effective niche overlap

Hence a greater number of effective niche dimensions provides a greater potential for diffuse competition.

When overlaps along the three dimensions are multiplied, the vast majority of interspecific pairs overlap very little or not at all

stronger diffuse competition requires greater average niche separation among coexisting lizard species. Low overlap with lots of competitors may be similar to high overlap with fewer interspecific competitors.

empirical results presented here support the niche overlap hypothesis, which predicts that maximal tolerable niche overlap should decrease with increasing intensity of competition.

**Schoener, T.W. (1983). Field Experiments on Interspecific Competition. *The American Naturalist* 122(2): 240-285**

The study of interspecific competition has long been one of ecology’s most fashionable pursuits

Ecologists have gathered numerous data on the ways species competitively coexist or exclude one another (reviews: Schoener 1974b, 1983)

Many of the putatively supportive observations have been challenged as being statistically indistinguishable from random contrivance – this paper sets out to show that this is not the case probs driven by what seems a rather personal view of the writer and it may indeed be true that he is right but the seed of doubt about the ubiquiotousness of interspecific competition is present

How do generalisations from field experiments compare with those of field observations?

I consider an interspecific competition experiment to be a manipulation of the abundances of one or more hypothetically competing species. Such manipulations can be removals, introductions or both

In the field, extrinsic, like intrinsic factors, are mostly uncontrolled, and these too can overturn our expectations.

In short we perform competition experiments in the field to find out if and how processes operate there in the presence of possibly overriding factors and major natural factors are uncontrolled

An overwhelming fraction of experimental attempts to detect interspecific competition in the field did so: 148/164 or 90% demonstrate some form of competition which equates to 76% of species studied

Studies performed may not be a random sample - the file drawer problem e.g. most studies are done the temperate regions. i.e. those that are proposed to be least interesting from a biodiversity perspective and low in overall community competition

Few studies are listed of folivorous insects which are exceptionally specious ~25% of all species

Traditionally, competition has been divided into two classes of mechanisms: exploitive and interference. This may not be a very exact way of dealing with this and this guy has proposed 6 different classes of competition.

The best that describes the one at play in the dung beetles is Consumptive competition: competition occurs when some quantity of resource is consumed by an individual, thereby depriving other individuals of it. 43 cases of competition in animals are consumptive

Few experiments showed year to year variation in the existence of competition despite the hypothesis of Wiens 1977 theory but many more showed that the intensity of competition could vary temporally.

**Schoener, T.W. (1974). Resource Partitioning in Ecological Communities. *Science* 185: 27-39**

Biologists have long been intrigued by differences in morphology and habit amoung closely realted species. Ecologists especially have concentrated on differences in the way species in the same community utilise resources.

The major pourpose of resource portioning studies is to analyse the limits interspecific competition place on the number of species that can stably coexist

Lab experiemmts of Gause and other have shown that when forced together one comeptiing species ca cause the extinction of the other competitor – Gause’s exclusion principle

To prove that a particular dynamic operates, one must perturb the system away from equilibrium by adding or removing individuals – however they do not show the mechanism of competition but this could easily and acuratly be summised

These type of experiemnts shed very little light on the origin of the differences – this is the problem with our study, we can suggest but not know – this is way I did the grant proposal

Studies heavily favour terrestrial vertabrates – reflection of the literature

It is either necessary or convientent to estimate resource differences by using species chracteristics, usually morphological ones – such as guild in DBs

Levins (32) and MacArthur (33) argue that in a competitive system, as the no. of species accumulates, those species will eventually have to segregate on more and more dimensions to preserve minimal resource overlap.

Cases of complementarity involve nearly all possible combinations of kinds of dimesions: 1) food type and habitat (not in DBs), 2) food type and time (DBs have shown this), 3) habitat and time

Many otherwise similar species are separated, often with extraordinarily small overlap, in geographical range.

We need a theory of resource partitioning as it relates to particular dimensions

Habitat dimesions are imoprtnat more often than food-type dimesions which are more often than temporal dimensions

Competition changes the value of feeding in a patch per unit time

Terrestrial pokilotherms (like DBs) relatively often partition fod by being active at diferent times of day

To understand resource portioning, essentially a community phenomenon, we require a holistic theory that draws upon models at the individual and population level

**Roberts, C.M. (1987). Experimental analysis of resource sharing between herbivorous damselfish and blennies on the Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology.* 111: 61-75**

Competition theory suggests that species with very similar resource requirements should not be able to coexist when resources are limiting. However, on coral reefs, territorial herbivorous fishes which use apparently very similar resources often coexist without competitive exclusion

The principle of competitive exclusion states that under conditions where one or more resources are limiting, species using those resources in a similar way should not be able to coexist (Birch, 1957). Thus species within communities have been assumed to coexist through competitively driven niche ~erentiation (e.g., Ma~~hur, 1965).

(Sale, 1977) hypoesized that high species diversity is maintained by random recruitment of competitively “equal” species to fill unpredictably available space

Hence, coexistence between species is mediated not by resource partitioning but through stochastic processes preventing competitive exclusion (Sale, 1977).

This study was conducted on One Tree Reef at the southern end of the Great Barrier Reef during July and August 1985.

*Pomacentrus flavicauda* and *Salarias fasciatus* may coexist through partitioning of food resources. This could be either through selection of different foods, or by feeding on the same foods but from different parts of the areas in which they cohabit.

The possibility of competition for food or space between *Pomacentrusflavicauda* and blennies, primarily *Salariasfasciatus,* was tested by a removal experiment. – just like we did!!

These data, and those on feeding microhabitats (below) indicate that both these species depend to a large extent on filamentous algae for food. The feeding microhabitat study showed little evidence of partitioning of food resources.

The manipulations thus appear to have had no significant effect on the behaviour of either *Pomacentrus* or *Salarias fascia&s* and hence this experiment failed to detect evidence of competition for food or space between these species.

changes in territory size and feeding rates of *P.flavicauda* gave no indication of exploitation competition with *Salarias fasciutus.*

Why are not these species competing when their space and food requirements seem so similar? The feeding microhabitat study showed little evidence of partitioning of the algal resource within areas of overlap. However, this does not preclude the possibility that damselfish and blennies are selecting different species of algae.

**####EXAMPLE OF INTERSPECIFIC RESOURCE SHARING!!!!!**

**Connell, J.H. (1961). The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle *Chthamalus stellatus*. *Ecology* 42(4): 710-723**

Most of the evidence for the occurrence of interspecific competition in animals has been gained from laboratory populations

Indirect evidence exists, however, which suggests that competition may sometimes be responsible for the distribution of animals in nature

When animals with similar requirements are found coexisting in the same area, careful analysis indicates that they are not actually competing with each other (Lack 1954; MacArthur 1958)

Chtamalus stellatus is present on the upper shore and semibalanus balanoides on the lower shore – despite the fact that Cs can grow on the lower shore.

The main purpose of this study was to determine the cause of death of those Cs that settled below the MHW

Intertidal barnacles are nearly ideal for the study of survival under natural conditions

In the nascence of balanus and thais the survival of Cs was good at all levels

For those Cs that had settled normally on the shore the survival was poorest in the lowest area (greatest immersion) - the same trend was seen for transplanted stones

At the upper shore margins of distribution Cs evidently can exist higher than balanus mainly as a result of its greater heat and dessciation tolerance

Of 167 deaths of Cs caused by competition for space, 161 were interspecific from balanus – interspecific competition between Cs and balanus was a most important cause of death in Cs

Above a certain level in the shore balanus has no effect on the survival of Cs

Due to its faster rate of growth balanus can cover a greater area more quickly than Cs and therefore come to dominate the rock surface

From all observations it appears that the poor survival of Cs below MHW is a result of crowding by dense pops of faster growing balanus

“Although animal communities appear qualitatively to be constructed as if completion were regulating their structure, even in the best studied cases there are nearly always difficulties and unexplored possibilities” (Hutchinson 1957)

The evidence presented in this paper indicates that the lower limit of the intertidal zone of Cs at Millport was determined by interspecific competition for space with Balanus.

**Tilman, D. (1987). The Importance of the Mechanisms of Interspecific Competition. *The American Naturalist* 129(5): 769-774**

Although there are differences in the reviews of schoener (1983) and Connell (1983) more than half of the species studied showed signs of interspecific competition

That more than 150studies were available for review is a testament to the dissatisfaction with which ecologists have viewed traditional studies that attempted to infer the presence if competition using correlational or distributional data

This guy questions whether previous experiments showing an increase in one species and a decrease in another can measure the importance of interspecific competition

In a natural community, one species may influence a second species both directly and indirectly

A press experiment is one where the densities of competitors are manipulated. This means that to fully understand the community the density of every species must be manipulated i.e. if 40 species = 40 experiments need to be carried out

Pulse experiments have also been suggested but are an unacceptable way to study resource competition

The existence of indirect effects means that there be no simple relation between the actual mechanism of pairwise interspecific interaction and the total effect of any given species has on another

Too much reliance on the Lokta-Volterra models – these are just models

This preoccupation with the phenomenon of competition, rather than with the underlying mechanisms, has occurred despite the frequent recognition that direct antagonistic interactions or direct density effects are rarely the proximate, much less the ultimate cause of competition

He considers a study on competition as mechanistic if it includes bothe direct process by which completion occurs and information on the physiology, morphology and behaviour of individual species or functional groups

For species to coexist stably there must be a trade-off in their physiological, morphological or behavioural traits

A study of competition requires a multifaceted approach that is both observational and experimental

Experiments that concentrate on the phenomenon of interspecific interactions, but ignore the underlying mechanisms, are difficult to intemperate and are of limited usefulness.

**Simberloff, D. and Dayan, T. (1991). The Guild Concept and the Structure of Ecological Communities. *Annual Review of Ecology and Systematics* 22: 115-143**

Original definition of guild in community ecology: defined as group of species that exploit the same class of environmental resources in a similar way. This term groups together species regardless of taxonomy that overlap significantly in their niche requirements. (Root 1967)

Root considered guild associates to be moulded by adaptation to the same class of resources but also by competition among themselves.

A parallel term for guild is ‘functional group’ coined (36) and widely used (67) for aquatic invertebrates – often used interchangeably with guild but not necessarily the same thing

Root’s 3 advantages to using guilds: 1) guilds focus attention on all sympatric competing species, regardless of their taxonomic relationship; 2) “Guild” eliminates the dual usage of the term “niche” as meaning both the functional role of a species and the set of conditions that permits a species to exist; 3) guilds are useful in the comparative study of communities.

‘guild’ has often been used in many different ways leading to confusion about its use

Use of the same resources may not imply competition for them

Experiment in sea urchins where the addition of one species did not have an effect on the feeding of two other species and if anything lead to higher fitness – facilitation (50)

The view of guilds as co-evolved entities , as “arenas of intense competition” is one reason the clear delination of guilds is important.

If guilds are not formed through competition but through autecological processes then the term of functional groups might be more appropriate

While investigators usually at least partly justify guild designations they often give the reader no clue about other sympatric species – not so much as problem where the whole community is dominated by dung beetles

The emphasis in animal community ecology has increasingly been on food resources as generating interspecific competition

Many studies define a guild as the group of species that inhabit a certain microhabitat

One advantage of the guild concept is that it focusses attention on all sympatric species involved in a potentially competitive interaction, regardless of their taxonomic relationships

Guilds can be formed of distantly related species that share resources

Most studies of guilds do not use quantitative methods to divide a group of species into guilds relying instead on taxonomy plus intuition.

It seems unlikely that any of the methods of assigning guilds quantitatively will become widely accepted.

What is defined as the ‘same’ class of resources (easily with dung) and what is ‘in a similar way’

- there seem to be lots of problems with the term guilds due to changes between habitats, time and the fact that it is a subjective category

Different investigators have divided the same or ecologically closely related taxa into guilds in different ways that reflect a different grasp of this term and different impression of a ‘similar way’ in guild definition

The popularity of the guild concept inevitably led to its use in environmental assessment and management

Stuff about the use of guild members as management and conservation tools - to much stuff to type but useful to back point about using guild rather than species for ecosystem function and service

**Montagnini, F. and Jordan, C.F. (2005). *Tropical forest Ecology* Springer**

Pages 40-67

Because energy moves faster through tropical systems it might also be expected that nutrients also cycle faster in tropical ecosystems

Nutrient cycling is higher in forests on fertile soil in the wet tropics than on infertile soil

Due to this quick cycling there is little free resources in the environment leading to the picture of rainforests as ‘resource deserts’

Therefore, patches of resource rich food will be sites of extreme competition.

## USE THIS REF FOR OTHER BASIC TROPICAL SYSTEM POINTS ##