

What can ant diversity-energy relationships tell us about land use and land change (Hymenoptera: Formicidae)?

Leticia RÍOS-CASANOVA & Brandon T. BESTELMEYER



Abstract

We identify and review an approach that views ant species diversity as a consequence of energy flux through an ecosystem. In this bottom-up view, energy apportioned to trophic guilds drives ant community responses to mesoscale variation generated by land-use and other processes. We introduce a conceptual model based upon this idea, and offer an interpretation of some data we have collected in the light of the model. Operationally, the concept focuses analysis upon the relationships between species richness / composition, trophic group identity, body size, and abundance. These attributes are compared among ecosystems that vary in total net primary productivity (NPP) and in how that productivity is divided among plant functional groups. We offer a brief example of how biomass and abundance of three ant trophic groups, large granivores, small granivores and scavengers, differed between two ecosystems that varied strongly in NPP patterns. We emphasize the value of linking ant measurements directly with NPP at mesoscales.

Key words: Ant community, ant diversity, ecosystem attributes, energy, functional groups, granivorous ants, macroecology, mesoscale, net primary productivity, review, scavenger ants.

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Introduction

Ants are important components of the Earth's biodiversity, so it is useful to know what structures that diversity and thereby how to conserve it (e.g., DUNN & al. 2007). In addition, by virtue of both the functional importance and diversity of ants, they should also tell us about status or health of the ecosystems in which they live. Consequently, ant communities have been used to evaluate the consequences of ecosystem characteristics such as climate, soil, vegetation, and disturbance regime (BESTELMEYER & WIENS 1996, SANDERS & al. 2003, FLOREN & LINSENMAIR 2005, GOVE & al. 2005, RÍOS-CASANOVA & al. 2006). The value of an ant-based ecosystem perspective, alone or as a complement to perspectives based on other taxa, has been forcefully argued and convincingly demonstrated (MAJER 1976, GREENSLADE & GREENSLADE 1984, ANDERSEN 1990, 1997, 2000).

In this paper our objective is to review an energy-based approach that links ant community functions and responses to variables including plant biomass and net primary production (NPP; KASPARI & al. 2000a) that are routinely used to measure the health of ecosystems. This perspective views ant species diversity as the result of energy flux through an ecosystem that is organized by primary producers and is subsequently apportioned to ant trophic guilds to drive ant community structure. This approach contrasts with habitat-based ant diversity studies addressing the role of

plant cover or vegetation structure in providing ecological niches for ant species. The energy-based approach does not directly consider the effects of habitat elements that affect foraging, predation or parasitism, events that disrupt the relationship between organisms and resources, or dispersal (ROSENZWEIG & ABRAMSKY 1993). Although it is certainly incomplete (like most individual themes), we argue that a bottom-up view allows ants to tell us a great deal about how ecosystems work and human impacts on those systems.

Below, we briefly review habitat and energy-based approaches to ant community variation, introduce a conceptual model for the energy-based approach, and offer an interpretation of some data we have collected in the light of the model (Box 1). While energy-diversity relationships are typically examined at global to regional scales (KASPARI & al. 2004), we focus here on their consequences at the scale of landscapes (e.g., a basin) that have been the targets of ant studies addressing land use issues.

Habitat-based approaches

The strong impact of vegetation structure on ant diversity is one of the central principles emerging from habitat-based ant community studies, particularly when contrasts between "open" and "closed" habitats are involved (HOFFMANN & ANDERSEN 2003). In these studies, microclimate and / or

nesting sites are often the direct, proximate mechanisms driving relationships between ants and vegetation structure. Indirect effects include competition from dominant species favored in certain microclimates that influences the activity patterns of subordinate species. For example, increases in vegetation cover alters species composition, reduces richness, and favors dominant species in Mediterranean woodlands (RETANA & CERDÁ 2000) and Florida forest (LUBERTAZZI & TSCHINKEL 2003) whereas richness alongside abundance of dominant species are favored in open habitats in Australian woodlands / grasslands (ANDERSEN 2003, BARROW & al. 2006).

Anthropogenic effects on ant communities also appear to be mediated largely by microclimate / nesting and related effects. For example, studies in which grazing-induced change in vegetation is not believed to significantly alter microclimate, such as in deserts, have found weak effects on ant communities (WHITFORD & al. 1999, BESTELMEYER & WIENS 2001a), but when grazing produces strong changes in vegetation structure and microclimate, effects on ant species composition can be large (BESTELMEYER & WIENS 1996). Similarly, fire-induced increase in the abundance of dominant species in Patagonian shrublands was associated with more xeric microhabitat conditions after fire (FARJIBRENER & al. 2002).

Fragmentation-induced changes in species composition in woodlands (DEBUSE & al. 2007) or reductions of species richness in tropical forest (CARVALO & VASCONCELOS 1999) have been directly attributed to increasingly open / xeric microclimate. Fragmentation edge effects in tropical forest may be ameliorated in older fragments surrounded by recovering vegetation (VASCONCELOS & al. 2006). Fragmentation effects can also be indirectly mediated by microclimate. Increases of an exotic ant (*Linepithema humile*) alongside competition-induced reductions in natives were related to fragmentation and specifically to increased moisture availability associated with urbanization (SUAREZ & al. 1998, MENKE & HOLWAY 2006). Similarly, increasing insolation in unshaded coffee monocultures can increase the dominant *Solenopsis geminata* and decrease ant diversity (PERFECTO & SNELLING 1995, PERFECTO & VANDERMEER 1996).

Energy-based approaches

A distinct set of studies have considered the relationship between ant communities and variables reflecting energy flux in ecosystems, typically taking place at regional to global scales. In a classical study, DAVIDSON (1977) found a strong positive relationship between granivorous ant diversity and rainfall (considered as a surrogate of productivity) at a regional scale in North American deserts. Recent studies have echoed this relationship and found that the abundance of ant colonies increases with productivity and mean temperature at global scales (KASPARI & al. 2000b) but that variation in NPP may be especially important in regions of generally low NPP (KASPARI & al. 2000a). GOTELLI & ELLISON (2002) found that latitude (a proxy for energy availability) is the most significant predictor of ant density across even a narrow range of latitude in New England, USA. The importance of elevation (SANDERS 2002, SANDERS & al. 2003) and latitude (BESTELMEYER & WIENS 2001a, b, PFEIFFER & al. 2003) on ant diversity has also been illustrated in other studies.

SANDERS & al. (2007), however, showed that productivity did not predict litter ant richness within the Great Smoky Mountains, USA, although temperature did. In a unique study of temporal patterns at a single site, KASPARI & VALONE (2002) found that the previous year's seed production was correlated to the abundance of granivorous ants, but that temperature determined the availability of that production to ants. These latter two interpretations indicate that energy has two distinct and interacting impacts on ant communities, via environment (specifically microclimate) on the one hand and via trophic relationships (productivity) on the other.

General concepts for an energy-based approach at landscape scales

Below we review a set of questions and concepts that can be used to consider the energy-based approach at the scales of landscapes typically considered in habitat-based studies of ant diversity. In doing so, we emphasize mechanisms that we suspect may be particularly important in such studies, and describe how habitat- and energy-based approaches can be linked. We also describe how questions can be framed based on this model.

How do ecosystems vary in energy capture?

Biodiversity is ultimately based on the energy fixed by plants and made available for biomass (growth, reproduction) and then to other trophic levels (net primary production or NPP; g of carbon m⁻² yr⁻¹). The amount of energy captured over time in a specific area depends on a host of factors including incident radiation, temperature, nutrient availability, and the capacity of plants to use those nutrients in production. Global variation in NPP is driven largely by differences in radiation, temperature, and climate. In contrast, landscape variation, nested within areas of similar global and regional radiation, is determined by 1) slope, aspect and therefore local radiation and water redistribution, 2) soils that determine water infiltration, storage, and uptake by plants, and 3) the history of land use or other disturbances that lead to persistent changes in plant community composition and sometimes soil properties (MONGER & BESTELMEYER 2006). Classifications of vegetation to alternative states within soil types coupled to widely available soil maps and hydrological models can be used to map landscape variation in NPP.

How is available energy apportioned to ant functional groups and species?

Differences in available energy in an ecosystem determine a number of key diversity patterns and subsequent feedbacks to ecosystems (WRIGHT & al. 1993). At global scales, energy may affect diversity through two mechanisms. Incident solar radiation (i.e., kinetic energy) governs environmental temperature and evapotranspiration, that in turn affects environmental suitability (e.g., via thermal tolerances) and metabolism. Alternatively, energy and water together govern NPP (potential energy) that determines resources to support organism abundance and body mass. The relative importance of these co-acting influences varies with latitude (HAWKINS & al. 2003) and also with scale. Following from the NPP patterns discussed above, one mechanism that is likely to produce variation within landscapes is captured in the "more individuals hypothesis" (SRIVASTAVA

Box 1: Contrasting ant communities between high and low productivity states in the Jornada Basin.

We compared the biomass and abundance of three functional groups of ants between two classes of vegetation states occurring at the Jornada Basin in the Chihuahuan Desert (southern New Mexico): shortgrass grassland (SG), and shrub-invaded bunchgrass grassland (SIBG; Box-Figs.). These two states are not alternatives of one another because they occur on different geomorphic settings, but they represent two very different environments with respect to NPP and plant functional groups for this example.

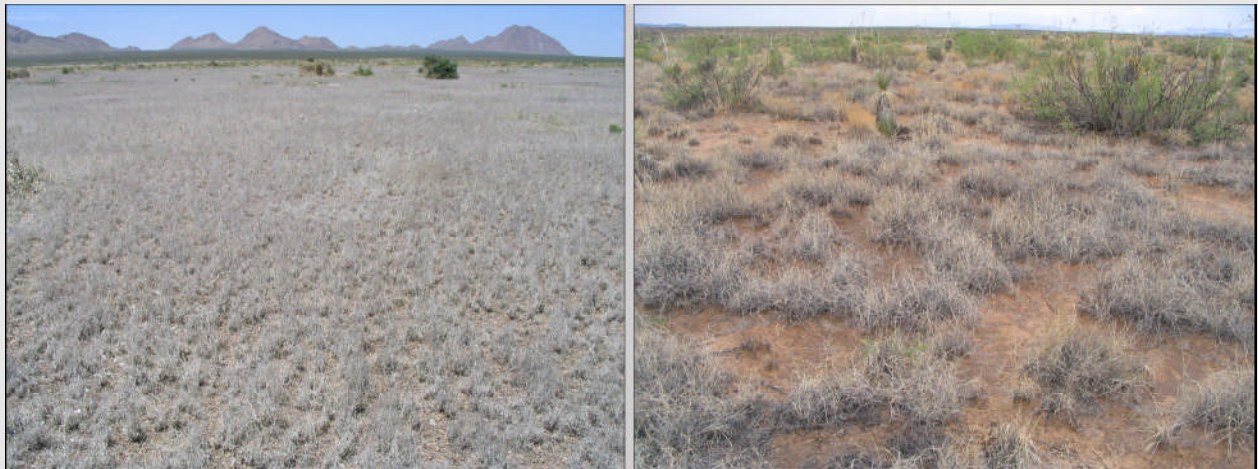
SG is dominated by burrograss (*Scleropogon brevifolius* PHIL.). It occurs on silt loam soils with well-developed biological and physical soil crusts that limit infiltration and production, while deeper clay horizons limit shrub invasion. SIBG occurs on loamy sand soils that impart high productivity when not degraded and diverse plant functional groups. The dominant grasses in this state are *Bouteloua eriopoda* TORR. and *Sporobolus flexuosus* THURB., and the dominant shrub is the mesquite *Prosopis glandulosa* TORR. Overall peak standing crop biomass (a proxy of NPP) estimated for fall 2007 (following HUENNEKE & al. 2001) ranged between 3.2 - 57.7 g/m² in four SG sites sampled, and between 107.8 - 155.6 g/m² in five SIBG sites sampled.

Ants were trapped over a 2-day period in September 2007 using a grid of 20 pitfall traps, 10 m spacing, at each site (9 total sites). Representatives of all ants were oven-dried and weighed using an analytical balance to 0.0001 g. We recorded a total of 22 species in SG and 24 species in SIBG. Each species was assigned to one of three functional groups according to SCHOOLEY & al. (2000): large granivores including *Aphaenogaster cockerelli* ANDRÉ, 1893 and *Pogonomyrmex desertorum* WHEELER, 1902; small granivores including several species in the genus *Pheidole* and *Solenopsis*; and scavengers including *Dorymyrmex bicolor* WHEELER, 1906, *Forelius pruinosus* (ROGER, 1863), and *Myrmecocystus mimicus* WHEELER, 1908. The species composition of the functional groups differed between the two states studied; they shared the most common species. Large granivores, small granivores and scavengers share respectively 50 %, 58 % and 26 % of species between both states.

Overall ant biomass estimated in SG was 1.49 ± 0.61 g and in SIBG was 0.96 ± 0.41 g and did not differ (Wilcoxon $W = 21$, two tailed $P = 0.41$). Total abundance was 845.5 ± 238.18 in the SG and 3928.4 ± 1651.96 in SIBG; the high variability precluded a statistical difference (Wilcoxon $W = 0.14$, two tailed $P = 0.19$). However, there were significant differences in the abundance and biomass of certain functional groups of ants between these states. Large granivores did not differ with respect to abundance (Wilcoxon $W = 19.5$, two tailed $P = 0.19$) although biomass was marginally higher in SG (Wilcoxon $W = 17$, two tailed $P = 0.06$). Small granivores were similar in biomass (Wilcoxon $W = 16$, two tailed $P = 0.41$) and numbers between states (Wilcoxon $W = 14$, two tailed $P = 0.19$). In contrast, scavengers had significantly higher numbers (Wilcoxon $W = 10$, two tailed $P = 0.014$) and biomass (Wilcoxon $W = 12$, two tailed $P = 0.05$) in SIBG, as we expected based on the presence of homoptera-bearing shrubs and stem-succulents (*Yucca* spp.).

Although vegetation of SIBG produces much more biomass than the vegetation of SG, neither ant biomass nor abundance differed systematically between the two states. Overall, we see that total ant and vegetation biomass are uncorrelated ($R^2 = 0.02$, $P = 0.07$, $N = 9$). This suggests that ants might be appropriating a larger fraction of available energy in the SG than in SIBG.

Differences emerge at the level of trophic functional groups. Large granivores, especially *A. cockerelli* and *Pogonomyrmex rugosus* EMERY, 1895, dominate the biomass in SG. These are species with large body sizes (0.002 - 0.003 g / individual) so they do not contribute much to overall forager abundance. These species are able to exploit the large seeds of certain perennials and annuals in this grassland. In contrast, dominant scavengers such as *D. bicolor*, *Forelius mccooki* (MCCOOK, 1880) and *F. pruinosus* are small (0.00003 - 0.0002 g / individual) but numerous in SIBG where they tend Homoptera primarily on mesquite bushes. Thus, our analysis points to the idea that shifts in ant functional group biomass may be related to shifts in the plant functional groups, but the total biomass of ants supported remains invariant (even as plant biomass varies between states). This assertion, of course, depends on the assumption that pitfall traps provide a reasonable comparative assay of ant biomass.



Box-Figs.: A burrograss (*Scleropogon brevifolius*) grassland on silt loam soils (left panel) and a black grama (*Bouteloua eriopoda*) - honey mesquite (*Prosopis glandulosa*) savanna on sandy loam soils (right panel), both located on the USDA-ARS Jornada Experimental Range, near Las Cruces, New Mexico in the Chihuahuan Desert, USA.

& LAWTON 1998); the more energy in NPP that is harvested by a taxon, the more individuals are supported, and that leads to more diversity and ecological dominance of that taxon. Recent concepts under the umbrella of the "metabolic theory of ecology" further highlight the role of body size, environmental temperature, and stoichiometry in mediating the relationship between NPP and abundance (BROWN & al. 2004). Illustrating some of these relationships, ENQUIST & al. (1998) found that plant productivity per unit area is a function of temperature but not the composition and size of plants; similar levels of productivity may occur in plant communities of vastly different species composition and plant mass if the temperature and rate of resource supply are similar among communities. Similar patterns related to "energetic equivalence" have been found in an animal community occupying a single site: loss of a large rodent species was compensated by a smaller species such that total energy use by rodents was similar over time (ERNEST & BROWN 2001).

The preceding ideas suggest three levels at which we can ask about how a taxon such as ants appropriates energy. First, we can ask how ecosystems vary in the proportion of energy flux through ants vs. other taxa as part of a total ecosystem budget. There were early attempts to do this in the International Biological Program in the 1960s - 1970s, but comparative data are limited. STAFFORD SMITH & MORTON (1990) speculated that the ecological dominance of ants and termites in Australia is driven by its characteristically low and variable resource availability that favors animals able to exploit such patterns. Unfortunately, however, we know of no contemporary efforts to estimate how the fraction of energy flux through ants versus other animals varies among ecosystems; all-taxon inventories should be able to accomplish this.

Second, we can ask how energy availability correlates with variation in ant mass, abundance, and diversity, similar to the approaches of Kaspari and colleagues (KASPARI & al. 2000a, b, 2004, KASPARI 2005) discussed earlier. Such correlations within landscapes, however, have rarely been examined (e.g., SANDERS & al. 2007). Work in other systems suggests that the nature and form of the relationship between NPP and diversity may differ across scales (CHASE & LEIBOLD 2002).

Third, we can ask how variation in energy produces variation in ant functional groups. This has not yet been examined. It would be fruitful to consider the relationship between NPP and ant abundance / diversity using various functional grouping schemes (ANDERSEN 2000, SCHOOLEY & al. 2000) considering the strategies that distinct groups use to exploit NPP. Ant researchers in tropical forests have used stable isotopes of N to demonstrate that the unexplained high abundance of arboreal ants is supported largely by the consumption of plant resources via homopteran exudate feeding and extrafloral nectaries, rather than predation (BLÜTHGEN & al. 2003, DAVIDSON & al. 2003). The ecological dominance of these ants (e.g., the dominant dolichoderines of ANDERSEN 2000) may, in turn, be driven by the large amount of carbohydrates consumed to obtain sufficient N from N-poor exudates. This energy is used in dominant behaviors and production of chemical weaponry (DAVIDSON 1998) that aids in the specialized use of homopteran populations to provide a steady supply of exudates (BLÜTHGEN & al. 2004). Changes in trophic position (and

therefore sources of energy exploited) over time may underlie the increasing dominance of some invasive ants (TILLBERG & al. 2007). In general, these studies suggest that stable isotope studies of ants alongside studies of changes in ant functional groups, the production in different plant functional groups, and specific resources such as insect prey and homoptera may provide a powerful way to understand how landscape variation structures ant diversity.

How is landscape change affecting the apportionment of energy to and within ants?

The energy-based approach asks how land-use practices affect total energy flux or energy flux through natural ecosystems and if there are consequences for biodiversity (VITOUSEK & al. 1986, WRIGHT 1990). Within Austrian agricultural landscapes, for example, HABERL & al. (2004) showed that human appropriation of net primary production was negatively correlated with species diversity.

Change in NPP within human-exploited natural systems, such as in forests, grasslands, or desert rangelands, may have a number of manifestations. Where soil degradation has occurred, NPP may be reduced (D.P.C. Peters & al., unpubl.) because water and nutrients become unavailable to plants where plant-soil feedbacks break down (RIETKERK & al. 2004). On the other hand, following from the concept of energetic equivalence, shifts to alternative states may alter the plant species and plant physiognomy contributing to NPP without much change in overall NPP. Finally, human impacts may alter the spatial distribution or size of plants and how their NPP is packaged, without substantially altering the composition of plants or NPP (e.g., MCCLARAN & ANGEL 2007).

These types of NPP changes may lead to changes in the energy available to support community-level abundance of heterotrophs (ALLEN & al. 2007). Changes in how that energy is packaged may lead to changes in ant diversity. Such changes may be mediated by the effects of NPP on food resources or on other habitat elements that determine access to those resources (such as nesting sites). These relationships suggest a profitable research avenue that links animal community and ecosystem ecology: (1) stratify a landscape or region in terms of potential NPP or how it is packaged in different plant functional groups (e.g., climate or soil gradients), (2) stratify areas of potential productivity into different land uses or alternative states (reflecting a legacy of past land-use impacts), (3) collect data on the NPP of those land-uses / states, (4) examine correlations among NPP of whole ecosystems or plant functional groups and metrics of ant abundance, body size, biomass, and species and functional group composition, and (5) identify key species or groups within which to conduct detailed analysis of trophic ecology via stable isotopes or to examine other interactions.

Viewed in this light, the use of ants as bioindicators can have new meaning. For example, when it is concluded that ants are poor indicators of land change because ant abundance and diversity are similar between "healthy" and "degraded" land types (e.g., WHITFORD & al. 1999), perhaps this indicates that in spite of changes in an ecosystem's appearance, the fluxes of energy in it have not changed substantially for ants. We can then ask a number of questions. Has overall NPP actually been reduced? If it has, has the proportion of this energy flux appropriated by ants (vs. other animals) increased to compensate for this loss? If so,

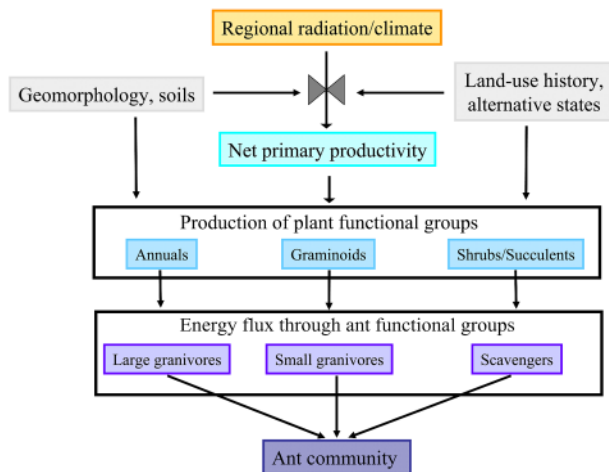


Fig. 1: Conceptual model of ant diversity-energy relationships for the Jornada Basin, New Mexico, USA. The large boxes are general classes of factor / processes and the smaller boxes within them represent subclasses specific to the Jornada Basin.

by what mechanism is this accomplished, by a shift in the plants used for food or nesting sites or the loss of a competing taxon? Studies in which ant communities reveal strong changes in species among land uses can be interpreted similarly. For example, we can ask if energy flux through the ant community has changed substantially, in spite of differences in species composition or ant numbers that is mediated by changes in ant body size.

Of course, there is a number of challenges to such research. Perhaps the greatest relates to our ability to estimate NPP of plants and the biomass and numbers of animals. Estimates of plant NPP are usually based on above-ground plant parts. NPP below ground may be substantial such that aboveground NPP may underestimate total NPP. This might be especially important for ants if they exploit below-ground resources (e.g., DAUBER & WOLTERS 2004). Similarly, a large proportion of ant biomass is found below-ground, often in deep nests, and conventional methods for ant community sampling miss this fraction. Until sufficient work is performed, we can only hope that variation observed in ground-foragers or surface-nesting ants via pitfall traps or intensive sampling adequately reflects differences in ant biomass. Finally, we often have little understanding of how the biomass of related consumers changes alongside ants, which can be difficult to estimate. In spite of these limitations, examining the relationships of ant diversity and NPP at landscape scales will broaden our interpretations of ant diversity data. We feel it would be productive to expand the conceptual basis of ant diversity responses from the traditional habitat and competition-based focus to embrace a broader spectrum of relationships.

A specific conceptual model for the Jornada Basin

We illustrate here how we are now thinking about ant communities in a Chihuahuan Desert ecosystem, the Jornada Basin in southern New Mexico, in light of the general concepts discussed above (Fig. 1). Although the details necessarily vary in different landscapes, we offer this model to show how the concepts can be assembled in a particular case.

The landscape we studied is about 100,000 ha comprising a variety of soils, from mid-Pleistocene, wind-worked sandy river deposits with thick petrocalcic horizons to Holocene calcareous or non-calcareous alluvium from two adjacent mountain ranges, respectively. Differences in soil texture and surface soil horizons cause differences in water infiltration and water holding capacity (DUNIWAY & al. 2007), and such differences can result in substantial differences in NPP.

As a function of land-use history and soils, overall NPP is represented by different functional groups of plants. Shrub-invasion and grass loss on sandy soils is well documented in the Jornada Basin as a consequence of historical heavy grazing and drought periods (PETERS & al. 2006). Consequently, grass-dominated, shrub-dominated, and mixed functional group states occur depending on land-use history. Soils condition the shift among states and how those shifts affect plant functional groups. Soils with clayey soil horizons, for example, seem to resist shrub invasion (BESTELMEYER & al. 2006) and instead witness a shift in perennial grasses during state changes.

The spatial grain of soil and vegetation state-derived heterogeneity encompasses whole ant communities. Although states may be patchy at fine scales, there are extensive areas 10s to 1000s of ha in size representing alternative states in the Jornada Basin (and throughout the southwestern USA). Thus, the energy flux through an ant population and community can reasonably be assumed to derive from the energy captured in the focal state where it is extensive.

State and soil-based differences in plant functional group composition result in different production of foods for functional groups of ants. Although soils and plants also affect nesting, foraging, and mating by microclimatic conditions (e.g., JOHNSON 2006), we can deemphasize these effects because at the Jornada site 1) we have observed that most ants (with exceptions, such as *Crematogaster*) can nest in a wide variety of places, 2) most ants, even thermophiles, can be crepuscular-nocturnal to avoid the heat of day in summer. We have focused on three plant functional groups that dominate Jornada communities and arid and semi-arid deserts of North America and Mexico in general: annuals, graminoids, and shrubs / succulents. Annual and large-seeded graminoid plants represent the main source of food to many larger granivore ants (PULLIAM & BRAND 1975, DAVIDSON 1977, PRICE & JOYNER 1997), whereas the small-seeded graminoids (that dominate Jornada plant communities) are used by small granivores (SCHOOLEY & al. 2000). Shrubs and succulent plants are among the most important sources of food to scavenger ants. Scavengers consume arthropods and insect cadavers opportunistically (e.g., after termite alate emergences), but most species feed continuously as herbivores, deriving carbohydrates and nitrogen from insect secretions and plant exudates. Shrubs and succulents are the source of these two resources (WISDOM & WHITFORD 1981, BESTELMEYER 2005). Consequently, the distribution, abundance and productivity of these three groups of plants thus are likely to be correlated with the functional groups of ants comprising an ant community in predictable ways (Box 1).

Conclusions

The study of ant communities can be approached from varying points of view, and it is likely that habitat-based and energy-based factors act together to structure ant com-

munities. In measuring the latter factors, we feel there is great value in linking ant diversity metrics, and particularly metrics of functional groups, to core ecosystem metrics such as plant biomass and NPP. We also advocate the consideration of ant biomass alongside measurements of abundance and richness and a greater consideration of ant trophic ecology in the interpretation of these interrelationships. This traditionally "macroecological" perspective may be especially useful at the landscape scale and lead to the recognition of interesting patterns that are not apparent in purely habitat-based perspectives.

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Zusammenfassung

Wir beschreiben einen Forschungszugang, der die Diversität von Ameisenarten als Resultat des Energieflusses durch ein Ökosystem betrachtet, und bieten dazu einen Überblick über den aktuellen Kenntnisstand. Gemäß dieser "bottom-up"-Sichtweise bedingt die, auf die trophischen Gilden aufgeteilte, Energie die Reaktionen der Gemeinschaft auf Veränderungen in einem mittleren räumlichen Maßstab, die auf Landnutzung und andere Prozesse zurückgehen. Wir stellen ein konzeptuelles Modell vor, das auf dieser Idee beruht, und präsentieren die Interpretation von Daten, die unter dem Gesichtspunkt des Modells zusammengetragen wurden. Die Vorgangsweise des Konzepts ist, Analysen auf die Beziehungen von Artenreichtum / Artenzusammensetzung, Identität trophischer Gruppen, Körpergröße und Abundanz auszurichten. Diese Charakterisierungen werden zwischen Ökosystemen verglichen, die sich in der Gesamtnettoprimärproduktion (NPP) unterscheiden, sowie darin, wie NPP auf funktionelle Gruppen von Pflanzen aufgeteilt ist. In einem kurzen Beispiel zeigen wir wie sich die Biomasse und Abundanz dreier trophischer Gruppen von Ameisen – große Granivore, kleine Granivore und Aasfresser – zweier Ökosysteme mit stark unterschiedlichen NPP Mustern unterscheiden. Wir betonen, wie wichtig es ist, Daten zu Ameisen direkt mit NPP und in einem mittleren räumlichen Maßstab in Beziehung zu setzen.

References

ALLEN, A.P., GILLOOLY, J.F. & BROWN, J.H. 2007: Recasting the species-energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity. In: STORCH, D., MARQUET, P. & BROWN, J.H. (Eds.): *Scaling biodiversity*. – Cambridge University Press, Cambridge, MA, pp. 283-299.

ANDERSEN, A.N. 1990: The use of ant communities to evaluate change in Australian terrestrial ecosystems: a review and a recipe. – *Proceedings of the Ecological Society of Australia* 16: 347-357.

ANDERSEN, A.N. 1997: Using ants as bioindicators: Multiscale issues in ant community ecology. – *Conservation Ecology* 1: article 8.

ANDERSEN, A.N. 2000: A global ecology of rainforest ants: functional groups in relation to stress and disturbance. In: AGOSTI, D., MAJER, D.J., ALONSO, L. & SCHULTZ, T. (Eds.): *Ants: stan-*

ard methods for measuring and monitoring biodiversity. – Smithsonian Institution Press, Washington, DC, pp. 25-34.

ANDERSEN, A.N. 2003: Ant biodiversity in Arid Australia: productivity, species richness and community organization. – *Records of the South Australian Museum Monograph Series* 7: 79-92.

BARROW, L., PARR, C.L. & KOHEN, J.L. 2006: Biogeography and diversity of ants in Purnululu (Bungle Bungle) National Park and Conservation Reserve, Western Australia. – *Australian Journal of Zoology* 54: 123-136.

BESTELMEYER, B.T. 2005: Does desertification diminish biodiversity? Enhancement of ant diversity by shrub invasion in southwestern USA. – *Diversity and Distributions* 11: 45-55.

BESTELMEYER, B.T., WARD, J.P. & HAVSTAD, K.M. 2006: Soil-geomorphic heterogeneity governs patchy vegetation dynamics at an arid ecotone. – *Ecology* 87: 963-973.

BESTELMEYER, B.T. & WIENS, J.A. 1996: The effects of land use on the structure of ground-foraging ant communities in the Argentine Chaco. – *Ecological Applications* 6: 1225-1240.

BESTELMEYER, B.T. & WIENS, J.A. 2001a: Ant biodiversity in semi-arid landscape mosaics: the consequences of grazing vs. natural heterogeneity. – *Ecological Applications* 11: 1123-1140.

BESTELMEYER, B.T. & WIENS, J.A. 2001b: Local and regional-scale responses of ant diversity to a semi-arid biome transition. – *Ecography* 24: 381-392.

BLÜTHGEN, N., GEBAUER, G. & FIEDLER, K. 2003: Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. – *Oecologia* 137: 426-435.

BLÜTHGEN, N., STORK, N.E. & FIEDLER, K. 2004: Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic. – *Oikos* 106: 344-358.

BROWN, J.H., GILLOOLY, J.F., ALLEN, A.P., SAVAGE, V.M. & WEST, G.B. 2004: Toward a metabolic theory of ecology. – *Ecology* 85: 1771-1789.

CARVALHO, K.S. & VASCONCELOS, H.L. 1999: Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. – *Biological Conservation* 91: 151-157.

CHASE, J.M. & LEIBOLD, M.A. 2002: Spatial scale dictates the productivity-biodiversity relationship. – *Nature* 416: 427-429.

DAUBER, J. & WOLTERS, V. 2004: Edge effects on ant community structure and species richness in an agricultural landscape. – *Biodiversity and Conservation* 13: 901-915.

DAVIDSON, D.W. 1977: Species diversity and community organization in desert seed-eating ants. – *Ecology* 58: 711-724.

DAVIDSON, D.W. 1998: Resource discovery versus resource domination in ants: breaking the trade-off. – *Ecological Entomology* 23: 484-490.

DAVIDSON, D.W., COOK, S.C., SNELLING, R.R. & CHUA, T.H. 2003: Explaining the abundance of ants in lowland tropical forest canopies. – *Science* 300: 969-972.

DEBUSE, V.J., KING, J. & HOUSE, A.P.N. 2007: Effect of fragmentation, habitat loss and within-patch habitat characteristics on ant assemblages in semi-arid woodlands of eastern Australia. – *Landscape Ecology* 22: 731-745.

DUNIWAY, M., HERRICK, J.E. & MONGER, H.C. 2007: The high water-holding capacity of petrocalcic horizons. – *Soil Science Society of America Journal* 71: 812-819.

DUNN, R.R., SANDERS, N.J., FITZPATRICK, M.F., LAURENT, E., LESSARD, J.-P., AGOSTI, D., ANDERSEN, A.N., BRUHL, C., CERDA, X., ELLISON, A.M., FISHER, B.L., GIBB, H., GOTELLI, N.J., GOVE, A., GUENARD, B., JANDA, M., KASPARI, M., LONGINO, J.T., MAJER, J., MCGLYNN, T.P., MENKE, S.B., PARR, C.L., PHILPOTT, S.M., PFEIFFER, M., RETANA, J., SUAREZ, A.V. & VASCONCELOS, H.L. 2007: Global ant biodiversity and biogeogra-

- phy – a new database and its possibilities. – *Myrmecological News* 10: 77-83.
- ENQUIST, B.J., BROWN, J.H. & WEST, G.B. 1998: Allometric scaling of plant energetics and population density. – *Nature* 395: 163-165.
- ERNEST, S.K.M. & BROWN, J.H. 2001: Homeostasis and compensation: the role of species and resources in ecosystem stability. – *Ecology* 82: 2118-2132.
- FARJI-BRENER, A.J., CORLEY, J.C. & BETTINELLI, J. 2002: The effects of fire on ant communities in north-western Patagonia: the importance of habitat structure and regional context. – *Diversity and Distributions* 8: 235-243.
- FLOREN, A. & LINSENMAIR, K.E. 2005: The importance of primary tropical rain forest for species diversity: an investigation using arboreal ants as an example. – *Ecosystems* 8: 559-567.
- GOTELLI, N.J. & ELLISON, A.M. 2002: Biogeography at a regional scale: determinants of ant species density in new England bogs and forests. – *Ecology* 83: 1604-1609.
- GOVE, A.D., MAJER, J.D. & RICO-GRAY, V. 2005: Methods for conservation outside of formal reserve systems: the case of ants in the seasonally dry tropics of Veracruz, Mexico. – *Biological Conservation* 126: 328-338.
- GREENSLADE, P.J.M. & GREENSLADE, P. 1984: Invertebrates and environmental assessment. – *Environment and Planning* 3: 13-15.
- HABERL, H., SCHULZ, N.B., PLUTZAR, C., ERB, K.H., KRAUSMANN, F., LOIBL, W., MOSER, D., SAUBERER, N., WEISZ, H., ZECHMEISTER, H.G. & ZULKA, P. 2004: Human appropriation of net primary production and species diversity in agricultural landscapes. – *Agriculture, Ecosystems and Environment* 102: 213-218.
- HAWKINS, B.A., FIELD, R., CORNELL, H.V., CURRIE, D.J., GUEGAN, J.F., KAUFMAN, D.M., KERR, J.T., MITTELBACH, G.G., OBERDORFF, T., O'BRIEN, E.M., PORTER, E.E. & TURNER, J.R.G. 2003: Energy, water, and broad-scale geographic patterns of species richness. – *Ecology* 84: 3105-3117.
- HOFFMANN, B.D. & ANDERSEN, A.N. 2003: Responses of ants to disturbance in Australia, with particular reference to functional groups. – *Austral Ecology* 28: 444-464.
- HUENNEKE, L.F., CLASON, D. & MULDAVIN, E. 2001: Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. – *Journal of Arid Environments* 47: 257-270.
- JOHNSON, R.J. 2006: Biogeographical parallels between plants and ants in North American deserts (Hymenoptera: Formicidae; Spermatophyta). – *Myrmecological News* 8: 209-218.
- KASPARI, M. 2005: Global energy gradients and size in colonial organisms: worker mass and worker number in ant colonies. – *Proceedings of the National Academy of Sciences of the United States of America* 102: 5079-5083.
- KASPARI, M., ALONSO, L. & O'DONNELL, S. 2000a: Three energy variables predict ant abundance at a geographical scale. – *Proceedings of the Royal Society of London B* 267: 485-489.
- KASPARI, M., O'DONNELL, S. & KERCHER, J.R. 2000b: Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. – *American Naturalist* 155: 280-293.
- KASPARI, M. & VALONE, T.J. 2002: On ectotherm abundance in a seasonal environment – studies on a desert ant assemblage. – *Ecology* 83: 2991-2996.
- KASPARI, M., WARD, P.S. & YUAN, M. 2004: Energy gradients and the geographic distribution of local ant diversity. – *Oecologia* 140: 407-413.
- LUBERTAZZI, D. & TSCHINKEL, W.R. 2003: Ant community change across a ground vegetation gradient in north Florida's long-leaf pine flatwoods. – *Journal of Insect Science* 3: 21-38.
- MAJER, J.D. 1976: The maintenance of the ant mosaic in Ghana cocoa farms. – *Journal of Applied Ecology* 13: 123-144.
- MCCLARAN, M.P. & ANGEL, D.L. 2007: Mesquite and grass relationships at two spatial resolutions. – *Plant Ecology* 191: 119-126.
- MENKE, S.B. & HOLWAY, D.A. 2006: Abiotic factors control invasion by Argentine ants at the community scale. – *Journal of Animal Ecology* 75: 368-376.
- MONGER, H.C. & BESTELMEYER, B.T. 2006: The soil-geomorphic template and biotic change in arid and semi-arid ecosystems. – *Journal of Arid Environments* 65: 207-218.
- PERFECTO, I. & SNELLING, R. 1995: Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. – *Ecological Applications* 5: 1084-1097.
- PERFECTO, I. & VANDERMEER, J. 1996: Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. – *Oecologia* 108: 577-582.
- PETERS, D.P.C., BESTELMEYER, B.T., HERRICK, J.E., FREDRICKSON, E.L., MONGER, H.C. & HAVSTAD, K.M. 2006: Disentangling complex landscapes: new insights into arid and semiarid system dynamics. – *BioScience* 56: 491-501.
- PFEIFFER, M., CHIMEDREGZEN, L. & ULYKPAN, K. 2003: Community organization and species richness of ants (Hymenoptera/Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert. – *Journal of Biogeography* 30: 1921-1935.
- PRICE, M.V. & JOYNER, J. 1997: What resources are available to desert granivores: seed rain or soil seed bank? – *Ecology* 78: 764-773.
- PULLIAM, H.R. & BRAND, M.R. 1975: The production and utilization of seeds in plains grassland of southeastern Arizona. – *Ecology* 56: 1158-1166.
- RETANA, J. & CERDÁ, X. 2000: Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. – *Oecologia* 123: 436-444.
- RIETKERK, M., DEKKER, S.C., DE RUITER, P.C. & VAN DE KOPPEL, J. 2004: Self-organized patchiness and catastrophic shifts in ecosystems. – *Science* 305: 1926-1929.
- RIOS-CASANOVA, L., VALIENTE-BANUET, A. & RICO-GRAY, V. 2006: Ant diversity and its relationship with vegetation and soil factors in an alluvial fan of the Tehuacán Valley, Mexico. – *Acta Oecologica* 29: 316-323.
- ROSENZWEIG, M.L. & ABRAMSKY, Z. 1993: How are diversity and productivity related? In: RICKLEFS, R.E. & SCHLUTER, D. (Eds.): *Species diversity in ecological communities: historical and geographical perspectives*. – University of Chicago Press, Chicago, pp. 52-65.
- SANDERS, N.J. 2002: Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. – *Ecography* 25: 25-32.
- SANDERS, N.J., LESSARD, J.P., FITZPATRICK, M.C. & DUNN, R.R. 2007: Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. – *Global Ecology and Biogeography* 16: 640-649.
- SANDERS, N.J., MOSS, J. & WAGNER, D. 2003: Patterns of ant species richness along elevational gradients in an arid ecosystem. – *Global Ecology & Biogeography* 12: 93-102.
- SCHOOLEY, R.L., BESTELMEYER, B.T. & KELLY, J.F. 2000: Influence of small-scale disturbances by kangaroo rats on Chihuahuan Desert ants. – *Oecologia* 125: 142-149.
- SRIVASTAVA, D.S. & LAWTON, J.H. 1998: Why more productive sites have more species: an experimental test of theory using tree-hole communities. – *American Naturalist* 152: 510-529.
- STAFFORD SMITH, D.M. & MORTON, S.R. 1990: A framework for the ecology of arid Australia. – *Journal of Arid Environment* 18: 255-278.

- SUAREZ, A.V., BOLGER, D.T. & CASE, T.J. 1998: Effects of fragmentation and invasion on native ant communities in coastal southern California. – *Ecology* 79: 2041-2056.
- TILLBERG, C.G., HOLWAY, D.A., LE BRUN, E.G. & SUAREZ, A.V. 2007: Trophic ecology of invasive Argentine ants in their native and introduced ranges. – *Proceedings of the National Academy of Sciences of the United States of America* 104: 20856-20861.
- VASCONCELOS, H.L., VILHENA, J.M.S., MAGNUSSON, W.E. & ALBERNAZ, L.K.M. 2006: Long-term effects of forest fragmentation on Amazonian ant communities. – *Journal of Biogeography* 33: 1348-1356.
- VITOUSEK, P.M., EHRLICH, P.R., EHRLICH, A.H. & MATSON, P.A. 1986: Human appropriation of the products of photosynthesis. – *BioScience* 36: 368-373.
- WHITFORD, W.G., VAN ZEE, J., NASH, M.S., SMITH, W.E. & HERRICK, J.E. 1999: Ants as indicators of exposure to environmental stressors in North American desert grasslands. – *Environmental Monitoring and Assessment* 54: 143-171.
- WISDOM, W.A. & WHITFORD, W.G. 1981: Effects of vegetation change on ant communities of arid rangelands. – *Environmental Entomology* 10: 893-897.
- WRIGHT, D.H. 1990: Human impacts on energy flow through natural ecosystems, and implications for species endangerment. – *AMBIO* 19: 189-194.
- WRIGHT, D.H., CURRIE, D.J. & MAURER, B.A. 1993: Energy supply and patterns of species richness on local and regional scales. In: RICKLEFS, R.E. & SCHLUTER, D. (Eds.): *Species diversity in ecological communities*. – University of Chicago Press, Chicago, pp. 66-74.