FORUM

# The core–satellite species hypothesis provides a theoretical basis for Grime's classification of dominant, subordinate, and transient species

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## Introduction

Grime (1998) recently made a welcome attempt to provide a link between studies of plant diversity and ecosystem function. He suggested that categories of species that he referred to as dominants, subordinates, and transients have differing, but important, roles in ecosystems (referred from here on as the DST classification). Grime suggests that many characteristics of ecosystem function are disproportionately influenced by traits of the dominant species, but that subordinates and transients also may play critical, although sometimes temporary, roles in determining ecosystem function. We believe that incorporating dynamics into the role that diversity may play in ecosystem processes is an important conceptual advancement. Our goal in this Forum article is to enlarge Grime's DST classification by linking it to an existing model of community dynamics. Our hope is that this will promote the development of a broader, more generalized theory linking vegetation structure, function and dynamics.

Grime's (1998) DST classification explicitly invokes temporal dynamics into the relationship between diversity and function. Yet in his essay, Grime (1998) makes no mention of any dynamic models in the development of his DST classification, e.g. island biogeography theory (MacArthur & Wilson 1967), patch dynamics (Pickett & White 1985), carousel model (van der Maarel & Sykes 1993). We believe that one model in particular, the core–satellite species hypothesis (Hanski 1982a, 1991), provides an important theoretical basis for Grime's DST classification. It is our purpose in this Forum article to explore the similarities between the DST classification and the core–satellite species hypothesis (referred to from here on as the CSS hypothesis) and bring out some important differences. We believe that unifying these ideas has much to offer plant ecology, and that in combination,

these models have important ramifications for the conservation issues raised by Grime.

## Essence of the CSS hypothesis and similarity to the DST classification

The CSS hypothesis is a null metapopulation model proposed by Hanski (1982a, 1991) to explain the relationship between species local abundance and regional distribution. It proposes that the pattern of species' distributions in a region is bimodal, as seen in Fig. 1. Species fall into two distinct types: 'core' species, which are locally abundant and regionally common, and 'satellite' species, which are sparse and occur at only a few sites. A requirement of this model is that all the species considered are 'similar', in that they are all capable of establishing populations at the set of sites under consideration. Other premises are that regional dynamics is important, and that extinction and colonization may be due to either demographic or environmental stochasticity. Deterministic, metapopulation models assuming extinction–colonization dynamics (Hanski & Gyllenberg 1993) predict the bimodal distribution obtained in the CSS. Biomodality is obtained because of the 'rescue effect'; a strong coupling of regional and local dynamics where migration rate is increased and local extinction decreased as the fraction of occupied patches in a region increases (Gotelli 1991). Empirical studies have supported the patterns predicted by the CSS hypothesis at regional, within-community, and multiple-spatial and temporal scales (Gotelli & Simberloff 1987; Collins & Glenn 1990, 1991, 1997; Ely & Gibson 1996). Indeed, the nearly universal nature of the relationship between regional distribution and local abundance makes it an important characteristic of large-scale community structure (Gaston 1996) and leads it to being a fundamental assumption of many metapopulation models (Hanski 1982a; Brown 1984; Kolasa 1989). Thus, the CSS hypothesis predicts the existence of dominant and transient species, as does Grime (1998), but the CSS does not relate the occurrence of these species to any particular ecosystem function.

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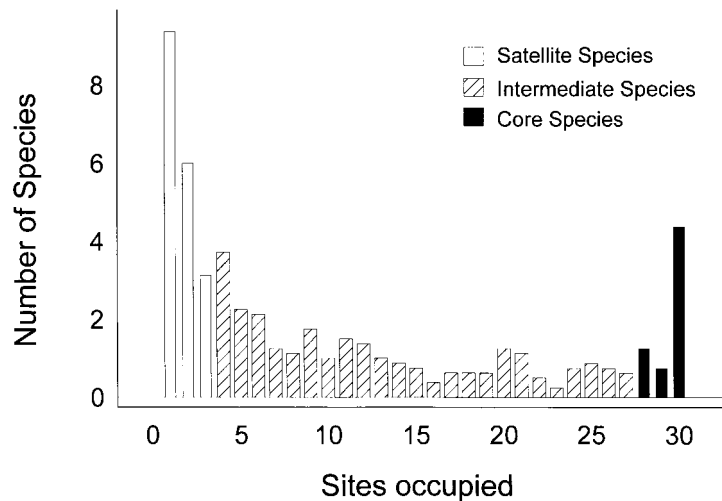
**Fig. 1** Illustration of the bimodal distribution of species according to the CSS hypothesis. These data are from an analysis of eight natural forest openings in southern Illinois, USA (J.S. Ely & D.J. Gibson, unpublished). Significant bimodality was established among all sites using curvilinear, polynomial regression (number of species = 6.6257−0.7041(number of sites) + 0.0191(number of sites)$^2$; $R^2 = 0.71$, $P < 0.0001$; $n = (8)$. Significant bimodality also existed at each site (data not shown). The allocation to satellite, intermediate and core species is shown.

Many of the fundamental properties of Grime's DST classification are very similar to Hanski's CSS hypothesis (see Table 1). One of the important differences is that the CSS as stated does not explicitly characterize species in the centre of the bimodal distribution (i.e. Grime's subordinate species). In the original CSS model, these species were assumed to be spatially dynamic, either increasing or decreasing regionally. A later version of the model (Hanski 1991) incorporated rural (locally distributed but abundant) and urban (widely distributed but sparse throughout) species to account for those species which did not fit directly into core and satellite categories. Another difference is that Grime (1998) suggests that transients (satellite species in CSS) are often juveniles of dominants at other sites but, because of its phenomenological derivation, CSS cannot make such a prediction. However, this does not make the models incompatible, since the CSS does allow species that are core species in some regions to be satellite species elsewhere. Also, quantitative metapopulation models do exist that incorporate local population structure and transient dynamics (e.g. Caswell & Cohen 1991). Coupling these models with models linking structure and function may provide a more general quantitative theory of dynamics, community structure, and ecosystem functioning.

**CSS forms the theoretical basis for DST: Both allow useful predictions**

As we note above, Hanski's CSS hypothesis has a mathematical basis that is lacking in Grime's DST classification (see Hanski 1982a, b). The CSS hypothesis is a null model that is falsifiable because it allows specific hypotheses to be erected and tested (Gotelli & Graves 1996). By contrast, Grime's DST classification is conceptual, and logical; it is derived from first principles by induction from the comparative biology of plants and their trade-offs in the scale and precision of resource foraging (Grime 1984; Campbell *et al.* 1991). Grime generalized his model using an idealized Whittaker dominance–diversity curve (his Fig. 1).

Despite differences in the derivation of the two ideas, we believe that both the CSS hypothesis and DST classification are essentially the same. What is of considerable interest and, we believe, of importance, are the differing interpretations obtained for each. The CSS hypothesis has been examined and tested as an hypothesis to explain the outcome of regional species extinction and colonization. Most recently, it has been found to be of value in understanding scaling issues amongst different types of organism (birds, grasshoppers, plants and small mammals: Collins & Glenn 1997). These authors predicted that core species might be particularly susceptible to the effects of habitat fragmentation. By contrast, the DST classification has not yet been tested (in its original form, although we contend that it has in its alias as the CSS).

A serious problem with the DST classification as stated, and of many attempts to link diversity with function, is that of scale dependence. Ecosystem processes operate at multiple scales and are certainly not limited to the scale of the usual $1\,m^2$ plot, a scale at which plant communities tend to be highly

**Table 1** Comparison of Grimes DST classification and Hanski's CSS hypothesis of community composition

| | DST | CSS |
|---|---|---|
| Dominant/Core species | Recur in particular vegetation types. Large, coarse-grained foraging, substantial contribution to biomass. | Regionally common, > 90% of habitat patches. Locally abundant. |
| Subordinate species | High fidelity, small in stature, occupy microhabitats. | Not explicitly characterized, but similar to subordinates by exclusion. Implied within the model as those species occupying 10–90% of habitat patches (i.e. classed as intermediate species in Fig. 1. |
| Transient/Satellite species | Low abundance and persistence. Lack fidelity to vegetation types. | Sparse, occur at only a few sites, ≤ 10% of habitat patches. |
| Dynamics | Transients often juveniles of dominants from other vegetation types. | Important. Core and satellite species may switch roles. |
| Abundance/distribution relationship | Positive although not stated explicitly. | Positive |
| Species distributions | Not addressed. | Bimodal. |
| Species pool | Determined by diversity of transients. | 'Similar'. Must all be able to colonize sites in question. |

variable in both space and time (van der Maarel & Sykes 1993). This issue has, however, been explored for the CSS hypothesis (Collins & Glenn 1997) which has been linked to other dynamic, scale-dependent models of community structure (Collins *et al.* 1993; Hoagland & Collins 1997).

More recently, the CSS hypothesis has been shown to apply to temporal dynamics in tallgrass prairie vegetation subjected to different frequencies of fire (Collins, in press). This analysis yields an even more direct relationship between CSS and Grime's DST classification. This temporal analysis demonstrated that the species that persisted at a site over a 15-years time frame were typically dominants (high abundance averaged over time), and that transient species typically had low abundance values in those years in which they occurred. Despite the persistence of dominants, all grassland communities were undergoing directional change regardless of disturbance frequency. The implication is that plant communities change over time through appearance and disappearance of transient species, and changes in the abundance of the dominants, regardless of their persistence. Such changes may limit the strength of any temporal relationship between species diversity and ecosystem function.

Overall, we believe that Grime made valuable and important predictions about the dynamic relationship between diversity and ecosystem function in his presentation of the DST classification. He makes a strong argument that a few species contribute disproportionately to ecosystem function (good examples provided by Silander & Antonovics 1982; Huston 1997). Grime's argument about competitive dominants and their disproportionate influence on structure and function is related to the observation that competitive ability can be directly related to plant size (Gaudet & Keddy 1988). Grime also states that transient species are a source of colonizers following disturbance and that they can indicate the intensity of competition. Perhaps most importantly, Grime suggests that the subordinate species (a group not well recognized by the CSS hypothesis) act as biological filters during community assembly. These potential filter and founder effects suggested by Grime have important consequences for ecosystem function.

The CSS hypothesis, we suggest, provides a spatial and temporal, metapopulation dynamic explanation of Grime's DST classification. The bimodality predicted by the CSS allows the recognition of core and satellite species that are equivalent to Grime's dominant and transient species. This equivalence allows the impact of Grime's DST classification to be enlarged through incorporation of the deterministic features of the CSS hypothesis. In particular, immigration and extinction characteristics can now be incorporated in the DST. For example, in recognizing the important ecosystem functions ascribed to transient species in the DST, we should also accommodate the role of metapopulation dynamics (e.g. importance of the rescue effect to regional migration rates and extinctions) of the CSS hypothesis.

Thus, Grime's contribution to scaling up community level phenomena to address ecosystem function is particularly welcome, no matter what we wish to call any synthetic model that links the spatial and temporal patterns of species distribution, abundance and dominance.

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