To the Graduate Council:

I am submitting herewith a thesis written by Susan M. Harrell entitled "Spatio-temporal variability in keystone species and implications for quantifying interaction strengths." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Mathematics.

Louis J. Gross, Major Professor

We have read this thesis
and recommend its acceptance:

Accepted for the Council:

Associate Vice Chancellor and
Dean of The Graduate School

SPATIO-TEMPORAL VARIABILITY IN KEYSTONE SPECIES AND IMPLICATIONS FOR QUANTIFYING INTERACTION STRENGTHS

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ABSTRACT

The keystone species concept has helped advance food web theory, differentiating functional versus trophic roles and strong versus weak interactors. Although early work tended to neglect spatio-temporal variability within and among communities, recent empirical and theoretical work on interaction strength and community importance recognize the context dependency of species interactions. These include the effects of disturbance, productivity, species associations, temporal variability, and spatial scale on species interactions. Spatio-temporal variability in the density of a keystone species affects the persistence, spatial extent, and degree of community effects. Moreover, the spatial extent and resolution the examiner chooses may affect estimates of interaction strength and their interpretation. Sixteen model scenarios of a simple consumer-prey interaction were examined to assess the effects of spatial structure and scale on the measurement and interpretation of interaction strengths. Four common interaction strength indices (raw difference, community importance, Paine's index, and dominance index) were calculated for each simulation to determine patterns associated with each index. Model scenarios assessed the dependence of interaction strength on 1) the spatial distribution of predators, 2) the degree of predator and prey movement, 3) the spatial extent, resolution, and location of the study area, and 4) characteristics of the prey and predator populations, such as density and predator capture ability. Results indicate in general that interaction strengths were strongest when predators were uniformly distributed and weakest when predator distribution was limited, regardless of the length of the experiment. When high prey densities interfered with the ability of

predators to capture prey, however, interaction strengths for the different predator spatial distributions depended on the length of the experiment, initial prey density, and rarity of prey Interaction strengths also depended on the dispersal ability of prey, reflecting a balance between prey entering and escaping predator patches as the predator spatial distribution varied. The spatial extent examined should be large enough to account for the degree of prey and predator movement, otherwise interaction strengths may be overestimated. The most reliable estimate of interaction strength, when prey dispersal is not too high, is found by measuring prey and predator populations in the local area in which they interact, rather than taking an average over a large spatial area. Theoretical models, empirical studies, and management strategies should account for the effects of spatial structure and scale. Neglecting these effects can lead to underestimates or overestimates of interaction strength, and possible mis-identification of keystone species.

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CHAPTER 1

INTRODUCTION

Keystones: Functional importance and community impacts

The keystone species concept was originally coined by Paine (1969) and has been the subject of much criticism (Mills et al. 1993, Hurlbert 1997). Recently, the definition of keystone species has been clarified as those species whose effects on community structure, positive or negative, are much larger than would be predicted by their abundance or their biomass (Bond 1993, Power et al. 1996). This definition addresses the overuse and frequent misuse of the concept and fuses it with the less common but more general term 'foundation species' (Dayton 1971, Thorp and Bergey 1981, Hurlbert 1997). The keystone species concept has helped advance concepts of interaction strength, functional versus trophic webs, species introductions, and maintenance of biodiversity (Simberloff 1992, Mills et al. 1993, Menge et al. 1994), and implies a continuum of interaction strength (Hurlbert 1997, Vanclay 1999). Viewing the keystone species concept along a continuum of strong versus weak interactions has various advantages (Menge et al. 1994, Power and Mills 1995). These require taking account of the complexity of interactions, as well as the spatio-temporal variability and density dependence of impacts.

The effect of a species, or community importance (CI), is typically measured as the total effect on a community property when the species in question is removed

(Navarrete and Menge 1996, Power et al. 1996). Empirical studies often assess the impact of the keystone on a single or small group of species, but strong interactors should have pronounced effects on the entire community (Paine 1980). Community importance should ideally incorporate the fundamental properties of the community, such as richness, diversity, and productivity (Hurlbert 1997). Power et al. (1996) quantified community importance as the change in an ecosystem trait per unit change in species abundance:

$$CI = [d(trait)/dp]/[trait], \quad (1.1)$$

where p is the proportional abundance of the keystone. More commonly, the impact is measured by removing the keystone completely:

$$CI = [\text{change in trait}/\text{ trait in presence of keystone}] / [p], \quad (1.2)$$

where p is the proportional abundance (Power et al. 1996). Keystone species would have an absolute value of CI much greater than one.

Keystone species may have strong community effects by interacting strongly with individual species in their community. Interaction strength, the per capita effect of one species on the growth rate of another (Navarrete and Menge 1996), is more commonly examined in empirical (Navarrete and Menge 1996, Wootton 1997) and theoretical studies (Yodzis 1988, 1996) of food web interactions, but considerable controversy exists as to which measures are most appropriate (De Ruiter et al. 1995, Laska and Wootton 1998, Ruesink 1998) The appropriateness of an interaction strength index depends on the length of the study, as well as properties of the interacting populations (Berlow et al. 1999). Experiments where species densities are manipulated may not result in predicted outcomes when functional importance does not match up

with food web theory based on energy flow (Raffaelli and Hall 1996). Community importance and interaction strength are likely, but not necessarily, strongly correlated (Navarrete and Menge 1996, Power et al. 1996, Berlow et al. 1999).

The presence of strong interactors in communities has been demonstrated repeatedly, and keystone species are probably ubiquitous elements of ecosystems (Chapin et al. 1992, Holling 1992, Allison et al. 1996). The presence of keystone species might constrain communities to follow more predictable trends of assembly than communities composed of less strongly interacting species (Grover 1994). The loss of such a strongly interacting species with particular functional characteristics can have a great impact on the entire community (Paine 1980, Wootton 1994, Chapin et al. 1997, Tilman et al. 1997). The variety of functional roles that species may occupy, including trophic, chemical, structuring, dynamical, and ecosystem effects (Chapin et al.1997, Tilman et al. 1997), contributes to the diverse classification of keystone species (Mills et al. 1993, Power et al. 1996). Keystone predators typically maintain diversity by preventing competitive exclusion by dominant prey species (Paine 1969, Paine 1992). A more predator-tolerant species (high ratio of reproductive to predation rate) can be considered a keystone prey if its introduction allows the stable coexistence of another species with a predator (Noy-Meir 1981). Keystone modifiers can have profound effects on the community by creating patches, causing disturbances, and facilitating decomposition (Jones et al. 1994, Lawton and Jones 1995). Keystone species can also have strong impacts as mutualists or resources (Gilbert 1980, Mills et al. 1993). A relatively rare species can have profound impacts by modifying the environment despite having small trophic effects (Naiman et al. 1986, Jones et al. 1994).

Keystone species have been referred to as functional groups without redundancy, that is, a group whose functional characteristics are undercompensated in its absence (Chapin et al. 1992). In many cases, a strong community-level effect may arise from a group of functionally similar species, rather than an individual species (Fleming 1985, Brown and Heske 1990, Power 1990, De Leo and Levin 1997). In the case of predation, Menge et al. (1994) classifies this as 'diffuse predation' and considers it as one extreme on a continuum of interactions, with keystone predation as the other extreme (Menge et al. 1994, Robles and Robb 1993). In some situations, functionally similar species may have only minor effects in the presence of a keystone (Belovsky and Slade 1993, Navarrete and Menge 1996). These species, however, may be able to compensate for the loss of the keystone (Allison et al. 1996, Navarrete and Menge 1996). Communities possessing functionally similar species with different environmental tolerances may experience increased stability due to such compensatory effects (Chapin et al. 1997). Even species that have a keystone effect on diversity within a particular community may be redundant in terms of ecosystem processes such as productivity or nutrient cycling (Lawton and Brown 1993). Consequently, measured values of community importance (CI; Eqs 1.1 and 1.2) may vary depending on the trait examined. CI values may still be useful in distinguishing keystone species, since species that have a strong influence on community structure are more likely to impact ecosystem properties than species that are weak interactors (Allison et al. 1996).

Clearly, not all species interact equally. Interaction strengths in real food webs are likely to be patterned in a way that promotes stability (De Ruiter et al. 1995). The majority of interactions in a community are likely to be weak to intermediate, decreasing

a community's vulnerability to invasion or extinction, and increasing its persistence and stability (MacArthur 1972, Lawton 1992, McCann et al 1998). Weak interactors may play a role in stabilizing natural communities because of high variability in their indirect effects (Berlow 1999). A few species within a community, however, are likely to be strong interactors or keystone species (Grabherr 1989, Paine 1992, Fagan and Hurd 1994, Power et al. 1996, Raffaelli and Hall 1996, Wootton 1997, McCann et al. 1998). This is in contrast to much of food web theory in which interaction strengths are often assumed to be uniformly distributed (Lawton 1992, Hall and Raffaelli 1993, Mills et al. 1993, Power et al. 1996).

The dichotomy of keystone versus non-keystone species within a community, however, may be an artifact of experimental limitations (Martinez and Dunne 1998). The community importance or interaction strength of species, including potential keystones, depends on the context of the experiment, as well as the spatial and temporal extent and resolution of the study. Consequently, the role of species, including keystones, should be placed in a continuum of interactions where small differences in the extent, strength, and duration of interactions separates the roles of organisms.

Context dependence of community impact

The interaction strength of species and the role of species as keystone is highly context-dependent (Power et al. 1996). The role of a species as keystone or its impact may differ between communities depending on properties of the interacting species, community, and environment (Paine 1980, Fauth and Resetarits 1991, Mills et al. 1993). The impact of a keystone species can consequently change over a short distance or over

time (Bond 1993). The functional role a keystone plays and the mechanism by which it impacts the community may also depend on properties of the community or environment (Hixon and Brostoff 1983, Foster and Schiel 1988, Kvitek et al. 1992). Most empirical research described here measures the impact or effect of keystone species or strong interactors through 1) high interaction strength with species in the community, or 2) considerable change in community composition, including abundance and richness, with the removal of the keystone. Such properties, while not necessarily correlated with each other or community importance (CI; Eqs. 1.1 and 1.2), illustrate the context dependence of keystone species.

The community impact of a keystone species depends on properties of the interacting populations (Fauth and Resetarits 1991). Body size of a keystone predator or its prey is an important determinant of interaction strength (Creed 1994, Dial and Roughgarden 1995). The impact of a keystone predator may also be affected by recruitment rates (Jackson and Kaufmann 1987, Antonelli and Kazarinoff 1988, Prince 1995, Allison et al. 1996, Robles 1997) or competitive abilities (Jackson and Kaufmann 1987, Grover 1994) of its preferred prey. Populations characterized by social interactions, such as aggregation (Antonelli and Kazarinoff 1988) or aggression (Palumbi and Freed 1988), can also affect the impact of a keystone species.

Species associations within a particular community can also affect the role of a species as keystone. The strength of a keystone's impact depends on the number of species who depend on it directly as well as through indirect links (Yodzis 1988, 1996, Jones et al. 1994, Abrams et al. 1996). Moreover, a strongly interacting species in one community may not be in a community where other species are present which can

compensate for its loss (Flecker 1997). A high degree of food web complexity or diversity reduces the likelihood that any one species will be a keystone (Thorp and Bergey 1981, Tanner et al. 1994). Keystone species may be more common when species diversity is low, reducing the probability that functionally similar species exist (Power et al. 1996). Additionally, the presence of predators of the keystone can diminish the effect of a keystone species on its community (Estes et al. 1998).

The productivity of the environment, degree of resource partitioning, and degree of disturbance affect the interaction strength and community impact of species (Thorp and Bergey 1981, Risch and Carroll 1982, Daily et al. 1993, Menge et al. 1994, Paul et al. 1995, Allison et al. 1996, Menge et al. 1996). The role of species as keystone often differs between disturbed and protected locations (Daily et al. 1993, Robles and Robb 1993, Menge et al. 1994, Menge et al. 1996). High frequency of disturbance may prevent potential effects of a keystone from reaching completion (Tanner et al. 1994). Environmental stress may exclude keystones from locations where they would potentially regulate community composition (Hart 1992). In the context of Huston's Dynamic Equilibrium hypothesis, namely that diversity is highest when the rate of competitive displacement is matched by the rate of mortality causing disturbances, keystone mutualists, whose presence reduces the mortality of interacting species, should have strong community impacts in situations of high mortality but low rates of competitive displacement (Huston 1994, Hacker and Gaines 1997). Keystone predators are likely to be important under conditions of low disturbance and high rates of competitive displacement (Thorp and Bergey 1981, Power 1992, Daily et al. 1993, Grover 1994, Huston 1994, Menge et al. 1996). Although periodic disturbances may have similar

impacts as keystone species (Menge et al. 1994, Power et al. 1996), in other cases, however, periodic disturbance is insufficient to maintain the role of a keystone (Collins et al. 1998).

Measuring interaction strength or community importance also depends on the time scale of the experiment (Berlow et al. 1999). For large bodied species or terrestrial communities, detecting large fluctuations in abundance may require long time frames (Brown and Heske 1990, Power et al. 1996). Long-term effects of species removal cannot be predicted from short-term observations (Yodzis 1988, 1996). Studies of keystone species must proceed long enough to exceed the frequency of disturbance events that may reset the community and to allow time for direct and indirect interactions to manifest (Valone et al. 1995, Power et al. 1996). Keystone processes can change among and within communities, hampering predictive abilities of investigators (Bond 1993).

Spatio-temporal variability in keystones

Knowledge about the spatial dynamics of species in a community is important for predicting patterns in food webs and the impact of keystone species (Lawton 1989, 1992, Navarrete and Menge 1996). Most populations possess some degree of spatial structure that can affect the impact of a potential keystone species. Variability in productivity and disturbance can affect the temporal and spatial distribution of a species and the strength of its interaction (Creed 1994). Small or long-term climate changes can cause shifts in the spatial and temporal distribution of species, consequently affecting the impact of keystone species (Sanford 1999). Additionally, the presence of predators or strong competitors may limit the spatial distribution of potential keystones and

weaken their effects on the community (Estes and Palmisano 1974, Wootton 1995). Spatial structure plays a large role in the effect of a keystone predator (Caswell 1978, Hastings 1978, Crowley 1979). The impact of a keystone modifier depends on the spatial distribution and temporal persistence of its constructs (Jones et al. 1994). The persistence of keystone resources, and consequently their impact on the community, depends on the continuity, distribution, and turnover of the microhabitats on which it depends (Gilbert 1980).

Some communities may depend on the patch dynamics of strong interactors. Flowering and fruiting patterns of *Piper* plants are temporally and spatially separated, allowing them to share the same seed-dispersing bats without experiencing serious competition (Fleming 1985). Patch dynamics of fruiting plants also contribute to the diversity of understory birds (Levey 1988) Resources are not likely to play a keystone role in regions where they are widely scattered or unpredictable (Gautier-Hion and Michaloud 1989). The distribution of sapsuckers, and their role as keystone modifiers, depended on the distribution of aspen and willow (Daily et al. 1993).

Factors that spatially concentrate a strong interaction can have overall effects on community organization (Paine 1992). Light gaps in the forest canopy often create concentrated patches of resources and consumer species where critical interactions are likely to be intense (Gilbert 1980, Levey 1988). Maintenance of these gaps by disturbance is necessary to sustain the resources that structure such communities (Gilbert 1980, Levey 1988). Aggregation or the presence of other predators may concentrate predators, which could potentially have strong effects, into small patches (Estes and Palmisano 1974, Paine 1992, Wootton 1995) Sea urchins contribute to the patchiness of the

intertidal region by having particularly strong effects in the region surrounding the crevices they occupy (Fletcher 1987). However, in regions where sea urchins are relatively confined to their burrows, their overall impact on the community may be slight (Prince 1995).

Keystone species may also impact the community by affecting the spatial distribution of the species with which they interact. Keystone predators may increase diversity of prey species by affecting the spatial distribution of other potential predators (Hixon and Brostoff 1983). Predator-mediated coexistence may depend on migration of prey from environmental patches where predation might be too strong (Caswell 1978). High prey dispersal from predator-dense patches may weaken predator-prey interaction strengths (Fagan and Hurd 1994).

A high degree of spatial complexity can weaken the overall impact of a keystone species. The apparent rarity of keystone species in terrestrial systems and rivers may be explained, in part, by the spatial and trophic complexity of such systems (Thorp and Bergey 1981, Fagan and Hurd 1994). Spatial heterogeneity creates more potential refuges and diminishes competitive interactions, weakening the impact of keystone predators (Power 1992, Leibold 1996, Robson 1996).

There is a need to bridge across spatial scales in order to detect the importance of individual species on a community or ecosystem (Power and Mills 1995). The impact of a keystone species on a community depends on the spatial scale the examiner uses (Menge et al. 1994, Power et al. 1996, Hurlbert 1997). Generalist predators may be more likely to enhance regional species diversity, while specialist predators may be more likely to enhance local species diversity (Leibold 1996). Local density measures may

underestimate the impacts of species mobility (Navarrete and Menge 1996). Intrahabitat dispersal may be important in buffering predators against spatial heterogeneity in total prey availability (Fagan and Hurd 1994). Natural variation in local keystone density may buffer a community against broad-scale change (Fagan and Hurd 1994).

Keystone density and impact thresholds

The high degree of spatial, temporal, and community variability in the role of keystone species implies community impact depends on both the per capita effect and the density of the keystone species. Communities may exist in alternative stable states depending on the presence or absence of a keystone species (Mittelbach et al. 1995, Abrams et al. 1996). Keystone species are typically determined by examining properties of the community when it is removed (Navarrete and Menge 1996, Power et al. 1996). However, dynamical properties and density dependent effects of keystone species may be more important than its presence or absence (Paine 1974).

Interaction strength and the impact of keystone species are often found to vary with density (Fagan and Hurd 1994, Menge et al. 1994, Prince 1995, Menge et al 1996, Navarrete and Menge 1996, Ruesink 1998). Potential keystones may have a weak impact in communities where their abundance is particularly low (Gautier-Hion and Michaloud 1989, Daily et al. 1993). Temporal variability in cicada availability can affect their interaction strength and role as a keystone resource for birds (Andersen 1994). High spatial variability may offer refuges to prey species at low predator densities, contributing to the patchiness of the impact of a potential keystone predator (Ostfeld and Canham 1993). The community impact or interaction strength may be particularly

high when keystone species density is high (Duran and Castilla 1989, Fagan and Hurd 1994, Menge et al. 1994).

Theoretical models (Caswell 1978, Noy-Meir 1981, Leibold 1996) and empirical studies (Lubchenco 1983, 1985) have shown that the effect of a keystone species is generally greatest at intermediate predation intensities. Aggressive interactions among keystone predators may act to reduce predator density and increase migration, thus maintaining intermediate densities and the greatest keystone effect (Palumbi and Freed 1988). Predation on the keystone species may also help to maintain densities that promote diversity (Estes and Palmisano 1974, Wootton 1995, Estes et al. 1998). Keystone species may also play a role in keeping overall predation intensity at intermediate levels by excluding other predators (Hixon and Brostoff 1983).

The variability of keystone impacts and interaction strengths with changes in density implies that the effects of a species at one density cannot be used to predict its effects at another density (Abrams 1993, Ruesink 1998; Fig. 1, see Appendices). Interaction strengths are often assumed to involve constant per capita effects (Laska and Wootton 1998, Ruesink 1998). However, the per capita community impact resulting from a change in keystone density is likely to be a nonlinear function of keystone density (Goeden 1982, Fagan and Hurd 1994, Ruesink 1998). At high keystone densities, a large change in density may result in a small community changes (Goeden 1982; Fig. 1). However, at low densities, small reductions in keystone density may produce progressively larger changes in the community (Goeden 1982) Alternatively, there potentially exist threshold densities at which the impact of a keystone switches from strong to weak (Goeden 1982). The per capita effects of hermit crabs apparently cross a

threshold from weak to strong when consumption exceeds resource production (Ruesink 1998). Although little is known about critical thresholds of diversity (Chapin et al. 1992), the strength, occurrence, and density of such a threshold would likely depend on the densities of other species, environmental properties such as productivity and disturbance, and spatio-temporal variability in the keystone density.

The question of scale

While it is clear from the above that community impact and interaction strengths are associated with a variety of complex factors which interact and are variable in time and space, there has been little focus to date on explicit mechanisms to evaluate the spatial extent and grain of interaction strengths (Martinez and Dunne 1998). The emphasis on scaling issues in ecology (Levin 1992) has so far had little impact on the definition of keystone species, either in a theoretical context in which it may be appropriate to define community impact relative to the spatial extent of the interactions involved in the community, or in the context of field evaluations of interaction strengths. The GIS methodologies and remote sensing approaches which have fostered a landscape approach to community analysis have not as yet been brought to bear on questions such as. Is community impact or interaction strength scale-dependent? Are some types of keystone impacts more scale dependent than others? How directly do underlying habitat characteristics drive interaction strengths? Are there threshold effects in space such that below certain extents and grain of habitat characteristics the interaction strengths of a keystone drop precipitously?

While many of these questions are of theoretical interest, there are definite applied implications to such an analysis. Human impact as it affects spatial fragmentation of habitat has potential to either raise or lower interaction strengths. As one example of this, the role of alligators as keystones in the Everglades may change considerably in some regions due to planned alterations of the hydrology to 'restore' the system. Such alterations may raise water levels in some regions at times critical to nesting, reducing alligator breeding and through time reducing the maintenance of the alligator holes which act as refuges during drydowns. Evaluating the spatial impacts of management in ecosystems is relatively unexplored (Hof and Bevers 1998), and analyzing such impacts would likely require across trophic level modeling approaches (DeAngelis et al. 1998).

Conclusions

Communities may exist in alternative stable states depending on the presence or absence of a keystone species (Mittelbach et al. 1995, Abrams et al. 1996). While alternative stable states represent extremes, this idea neglects more subtle but important variation in the density and per capita effects of keystones, and the natural variability among communities at larger spatial extents (Foster and Schiel 1988). Trophic and functional webs are not static structures (Wilbur 1997). Spatial and temporal mechanisms interconnect webs, resulting in ongoing changes in species interactions within a community (Wilbur 1997). Densities of keystone species can vary both temporally and spatially, affecting their overall impact on the community. Changes in per capita effects can operate independently, or in concert, with changes in density

(Sanford 1999). Moreover, the impact of a rare keystone species may depend on the spatial resolution used by the examiner (Menge et al 1994). Reductions in the density of keystone species may be just as important as their removal. If minimum keystone densities exist where community flux remains low, this minimum density is likely to vary with properties of the community and environment, as well as spatially and temporally. However, if the impact of keystone species varies in a predictable way with spatial and temporal patterns of its density, then community predictions could be made with more certainty.

CHAPTER 2

METHODS

Background

Understanding how species interact in food webs is crucial in order to make predictions about natural communities. Pairwise interactions, such as competition, predation, and mutualism, can have profound direct and indirect effects throughout the food web depending on the connectedness of the food web and strength of interactions (Paine 1980, Abrams et al. 1996). The majority of interactions in a community are likely to be weak to intermediate, with only a few species having strong effects (Lawton 1992, Paine 1992, Fagan and Hurd 1994, Raffaelli and Hall 1996, Wootton 1997, McCann et al. 1998). Most of these studies use quantitative indices of "interaction strength", the per capita effect of one species on the growth rate of another, that are directly related to theoretical models, allowing for consistency and comparisons between empirical and theoretical studies (Laska and Wootton 1997).

Developing useful predictive models and reliable management and conservation strategies requires understanding the distribution and nature of interaction strengths within a community, including identifying strong interactors or keystone species (Mills et al. 1993, Power et al. 1996). Keystone species are species whose effects on community structure, positive or negative, are much larger than would be predicted by their abundance or biomass (Power et al. 1996). The variety of functional roles that species

may occupy, including trophic, chemical, structuring, dynamical, and ecosystem effects (Tilman 1997, Chapin et al.1995), contributes to the diverse classification of keystone species as predators, prey, mutualists, resources, or modifiers (Power et al. 1996, Mills et al. 1993). The interaction strength of species and the role of species as keystone is highly context-dependent, depending on properties of the interacting species, community, and environment (Paine 1980, Mills et al. 1993, Power et al. 1996). Frequent disturbances or changes in productivity can affect the impact of a strong interactor by preventing the community from reaching equilibrium or altering competitive strengths and resource availability (Power 1992, Huston 1994, Menge et al. 1994, Allison et al. 1996). The strength of a keystone's impact depends on the number of species who depend on it, the presence of predators, or the presence of functionally similar species (Jones et al. 1994, Abrams et al. 1996, Flecker 1997, Estes et al. 1998). Additionally, studies of keystone species must proceed long enough to allow time for direct and indirect interactions to manifest (Valone et al. 1995, Power et al. 1996). Consequently, different interaction strength indices may be appropriate for different empirical studies, depending on the length of the experiment, properties of the individual species, and equilibrium status of the community (Berlow et al. 1999). Less is known, however, about the effects of space and scale on interaction strengths.

Most populations possess some degree of spatial structure, and ecologists are becoming increasingly aware that dispersal, patchiness in distribution, and habitat spatial complexity all affect the way populations interact (Gilpin and Hanski 1991, Kareiva 1994, Holt 1996, Polis et al. 1996, Tilman and Kareiva 1997, Morin 1999). This heterogeneity in the distribution of populations can affect interaction strengths and the

community-level impact of strong interactors or keystone species. The spatial distribution of species can be affected by variability in productivity or disturbance (Creed 1994), the presence of predators or strong competitors (Estes and Palmisano 1974, Wootton 1995), or the spatial variability in habitat conditions and resources on which the species depends (Gilbert 1980). A high degree of spatial complexity can weaken the overall impact of a keystone species (Power 1992, Leibold 1996).

Moreover, there is a need to bridge across spatial scales in order to detect the impact of individual species on a community or ecosystem (Power and Mills 1995). Interaction strength and the measured impact of a keystone species likely depend on the appropriateness of the spatial area and resolution the examiner chooses (Menge et al. 1994, Power et al. 1996). Spatial area might be considered the size of the landscape, on the order of 100 to 10,000 m^2, and spatial resolution the size of an individual exclosure, on the order of 1 to 10 m^2 (Martinez and Dunne 1998). A coarse resolution or small spatial extent may discount individuals or populations that are affected by a keystone species. Experimental results for study sites of a particular spatial extent do not necessarily extend to larger or smaller spatial areas, and strong interactors at one spatial scale may appear to have weaker impacts when spatial extent or resolution are increased (Martinez and Dunne 1998). Understanding how interaction strength and community importance are affected by space and scale will improve our ability to project dynamics in natural food webs.

Objectives

Empirical and theoretical approaches to measuring interaction strength typically ignore the effects of space, measuring species density within a particular study site (Menge et al. 1994, Navarrete and Menge 1996, Raffaelli and Hall 1996) or utilizing non-spatial models (McCann et al. 1998, Vandermeer and Maruca 1998, Berlow et al. 1999). These studies inherently assume a uniform population density or assume effects of space are negligible. However, study sites with similar population densities may differ remarkably in population spatial structure. This may lead to misinterpretation of interaction strengths or the misclassification of species as keystone. Moreover, the spatial extent and resolution the examiner chooses may affect the interpretation of interaction strength or community importance (Menge et al. 1994, Martinez and Dunne 1998). Understanding the effects of space and scale will improve our ability to compare communities, interpret theoretical and empirical results, and determine appropriate management and conservation strategies.

Strong interactors or keystone species may occupy a variety of functional roles, but by definition will have pronounced effects on properties of the community, such as richness, abundance, or productivity (Paine 1980, Power et al. 1996). However, theoretical concepts of strong and weak interactors are currently better understood for a single consumer-prey interaction, as measured by indices of interaction strength (Laska and Wootton 1998, Berlow et al. 1999). Consequently, I used a simple, two species predator-prey model to analyze the effects of spatial structure and scale on interaction strength.

Assessing how spatial variability in the density of interacting consumer-prey populations affects interaction strength will improve our ability to consistently and accurately examine communities. In particular, the following are examined:

1) the dependence of interaction strength on the spatial distribution of predators, namely widespread predators versus those confined to patches,
2) the dependence of interaction strength on degree of interaction between predator and prey populations, as measured by prey movement or predator movement, and
3) the effect of the prey's ability to escape predator patches on interaction strengths

Furthermore, choosing study areas of an appropriate spatial extent can affect how interaction strengths are measured and interpreted, so I examine:

1) the dependence of measured values of interaction strength on the spatial resolution and spatial area examined, and
2) the effect of choosing a study site that does not incorporate the entire community, as measured by prey outside the study area interacting with populations inside the study area, on interpretation of interaction strength.

Additionally, an objective is to differentiate the effects of 1) characteristics of the predator population, such as rarity of predator, predator interference, or the ability of the predator to capture prey, and 2) characteristics of the prey population, such as rarity of prey, self-limitation of population growth, or nearness of the prey population to

equilibrium. Each of these may alter the effects of spatial structure on interaction strength.

Quantifying interaction strength

Several different quantitative measures have been used to empirically estimate the strengths of species interactions in food webs (Laska and Wootton 1998, Berlow et al. 1999). Interaction strengths are typically measured by comparing prey abundance when the predator is present at normal abundance to that when the predator is removed completely (Power et al. 1996). Prey and predator abundance are typically measured as densities, i.e. numbers of individuals per m^2.

For measuring predator interaction strength, perhaps the simplest measure is the raw difference (RD), or the absolute change in prey abundance per predator:

$$RD = (N - D) / Y , \qquad (2.1)$$

where N is the prey abundance in the presence of predators, D is the prey abundance when the predator is removed, and Y is the predator abundance (Berlow et al. 1999). The raw difference, a dimensionless quantity, has been used historically by field ecologists to show absolute treatment effects of predator removal on prey abundance (Connell 1961, Dayton 1971, Menge 1976, 1978).

Paine's Index (PI) of interaction strength measures the per capita effect of a predator on the per capita change in prey abundance:

$$PI = (N - D) / (D\,Y) , \qquad (2.2)$$

where N, D, and Y are as previously described (Paine 1992, Fagan and Hurd 1994, Raffaelli and Hall 1996). Under equilibrium conditions, Paine's Index is mathematically

equivalent to the per capita interaction strength used in Lotka-Volterra predator-prey equations (Laska and Wootton 1998), and thus provides a link between theoretical models and empirical studies. Unlike RD, PI is measured in units of density^{-1}, and is normalized by dividing by prey abundance in the absence of the predator.

Community Importance (CI) was originally conceived as an index to measure the impact of potential keystone species on a community or ecosystem trait such as richness, diversity, or productivity (Power et al. 1996). For purposes here, CI measures the proportional change in prey abundance per change in proportional abundance of the consumer:

$$CI = (N - D) / (N p_y) , \qquad (2.3)$$

where N and D are prey abundance in the presence and absence of the predator, and p_y is the proportional abundance of the predator before it was removed ($p_y=Y/(Y+N)$). Community Importance, unlike Paine's Index, is dimensionless. CI is calculated to normalize the predator impact by using its proportional abundance, and normalize prey density by dividing by the prey abundance in the presence of the predator (N).

The Dynamic Index (DI), like Paine's Index, links theoretical models to empirical measures of interaction strength. DI is based on the discrete-time version of the Lotka-Volterra equations, but unlike PI, makes no assumptions about equilibrium conditions (Osenberg and Mittelbach 1996, Wootton 1997). DI measures interaction strength as the difference in exponential prey growth rates with and without predators, assuming prey grow exponentially:

$$DI = ln(N/D) / (Y t) , \qquad (2.4)$$

where N, D are prey abundance with and without predators, Y is predator abundance before removal, and t is the time since predator removal. DI, measured in units of density^{-1}time^{-1}, is not normalized to predator density and depends on both time since perturbation and the measured units of time.

Simulation model

For a simple system of a single prey and single predator (e.g. Berlow et al. 1999), I examined the four measures of interaction strength using various spatial extents and different spatial patterns of predator density. The aim was to simulate a typical field experiment where a long-lived predator interacts with a prey species in a given area. The prey species is assumed to have a much shorter generation time than the predator.

The predator and prey populations interact on a grid of cells. Within each grid cell, local populations of predator and prey interact and grow. For all simulations, predator density was assumed to be constant, i.e. $dP/dt = 0$, within each grid cell over the course of a simulation . Prey dynamics were described as follows:

$$\frac{dN}{dt} = r\,N\left(1-\frac{N}{K}\right)-\frac{aNP}{1+c_N N+c_P P}\ , \qquad (2.5)$$

where N is prey abundance, P is predator abundance, r is prey per capita intrinsic growth rate, K is prey carrying capacity, a is predator attack rate, and c_N and c_P are parameters describing the functional response of the predator. The predator attack rate, a, is the theoretical interaction strength. Throughout the study, $r = 0.5$ and $a = 0.05$. Prey grow logistically toward carrying capacity K in the absence of predators, but suffer

mortality in the presence of predators. When $c_N = c_P = 0$, the predator has a Type I functional response with a constant per capita attack rate, *a*. If $c_N > 0$, the predator has a Type II functional response, a saturating function of prey density (Holling 1959). If $c_P > 0$, the predator functional response is a saturating function of predator density. In this case, predators interfere with the ability of other individuals to capture prey at high predator density.

The predator and prey populations interact on a rectangular grid of cells, dispersing from each cell to neighboring cells after each time step. Dynamics in a single cell were solved using a fourth-order Runge-Kutta method with the MapleV computer package. With each time step, individuals in the prey population undergo a cycle of breeding, dispersal, and mortality. After each time step, a proportion of the prey or predator population, described by the constants μ_{prey} and $\mu_{predator}$, respectively, migrates from a single cell to each of the neighboring 8 cells, where $0 \leq \mu_{prey} \leq 1$ and $0 \leq \mu_{predator} \leq 1$. The fraction of a cell's population that migrates to each neighboring cell is $\mu_{prey}/8$ or $\mu_{predator}/8$. The grid of cells has a closed boundary: prey do not enter or exit the grid from the edge. For prey (or predator) populations in edge or corner cells, only $5\mu_{prey}/8$ or $3\mu_{prey}/8$ of the prey population migrates to neighboring cells, respectively, with each neighboring cell receiving $\mu_{prey}/8$ of the prey population. Except in a single case where $\mu_{predator} > 0$, predators are assumed to not move between cells ($\mu_{predator} = 0$). Since prey disperse evenly to the surrounding neighbor cells, results presented here for a rectangular grid are expected to be qualitatively similar to those of a hexagonal grid, particularly if the fraction of prey dispersing to eight neighbors in the rectangular grid is similar to the fraction of prey dispersing to six neighbors in a hexagonal grid

For the cases described below, simulations of the model were run to obtain trajectories of the prey density with and without the predator Interaction strengths were calculated based on the average density of prey or predators across the entire spatial grid. This allows comparison of non-spatial models (Berlow et al. 1999) to the models developed here. Effects of spatial structure and scale can then be determined by eliminating problems due to changes in total population size that occur by adding space. Simulations were run for 40 time steps, which in most cases was sufficient time for spatial and temporal dynamics to reach equilibrium, i.e. prey populations in each grid cell were no longer changing over time. The four interaction strength indices were calculated at each time step to determine if the effects of space and scale on interaction strength changes over the course of an experiment.

Model scenarios

Simulations were run and predator interaction strengths were calculated for sixteen different model scenarios (Table 1). For most cases, predator and prey populations interacted on a 25 (5x5) cell grid where predator spatial structure was varied (Fig. 2). For each simulation, average initial prey and predator densities across the entire spatial grid were held constant. Prey density was always uniform across the entire grid (same population size in each cell) at the start of the simulation. Predators had a uniform density when present in all 25 cells. Additionally simulations were run with predators confined to 1, 2, 3, 4, 5, or 9 cells. In these cases, the average predator density across the entire spatial grid was the same as in the case of uniform density. However, the local density of predators within a single cell increased as predators were

confined to fewer cells (Table 2). Furthermore, for predators confined to 2, 3, 4, 5, or 9 cells, the spatial arrangement of the cells was varied to simulate predators that were clumped, arranged linearly, more spread out across the spatial area, or confined to boundary cells (Fig. 2). To determine the effects of predator location, the coefficient of variation (CV) in interaction strength among the different spatial arrangements (linear, clumped, spread, or very spread),

$$\frac{\text{mean interaction strength}}{\text{standard deviation in interaction strength}} \text{x100\%}, \qquad (2.6)$$

was calculated for a particular number of cells with predators (for example, the CV in interaction strength among 3 linear, 3 spread, and 3 very spread predators for a given model scenario).

Sixteen model scenarios were examined (Table 1, Table 3). In case 1, prey grow exponentially with no density dependence incorporated into the model. Case 1 assessed the degree to which spatial structure affected interaction strength for prey with no self limitation. In case 2, prey grow logistically and predator movement, in addition to prey movement, is allowed across the spatial grid. At the start of the simulation, predators were confined to 1, 2, 3, 4, 5, or 9 cells, but are allowed to disperse to neighboring cells with each time step. Case 2 assessed the degree to which predator movement modified the effects of space on interaction strength, and this was the only case in which local predator density varied over time. Cases 3 to 6 assessed the effects of spatial structure on interaction strength when prey grow logistically. For cases 3 and 4, sensitivity to prey initial density and its distance from carrying capacity was assessed. Cases 5 and 6

assessed effects of variability in initial prey density. Predators were added to the system when prey were at their carrying capacity ($N_0 = K$). These cases were analogous to an empirical study comparing prey communities differing in equilibrium abundance, such as among sites differing in productivity. In cases 4 and 6, the predator functional response was a saturating function of prey density Comparison of cases 3 to 4 and cases 5 to 6 allowed assessment of the degree to which predator functional response modified the effects of spatial structure on interaction strength. In cases 7 through 11, initial prey density and carrying capacity were held constant between simulations, but average predator density across the entire spatial grid was variable. In cases 7, 8, and 9, predator functional response was a linear function of prey density. In cases 10 and 11, however, predators were assumed to interfere with each others ability to capture prey at high predator densities ($c_P > 0$). Comparison of cases 7, 8, 9 to 10, 11 assessed the degree to which predator interference modified the effects of spatial structure on interaction strength.

To examine effects of spatial scale, for cases 8 and 11 simulations were run for a 49 (7x7) cell grid, in addition to the 25 (5x5) cell grid. Average predator density across the entire 49 cell grid was the same as the 25 cell grid, but local predator densities within a single cell were different (Table 2). The spatial arrangement of predators was identical to the 25 cell grid, with the addition of a border of prey, one cell wide, surrounding the grid. Four additional spatial arrangements were also considered for the 49 cell grid, as well as uniform density in all 49 cells (Fig. 2). For case 7, simulations were also run for a 9 (3x3) cell grid, with predators uniformly distributed across all 9 cells, or confined to 1,

2, 3, or 4 cells (Fig. 2). Comparison of cases 7, 8, 9 or 10, 11 assessed how the spatial scale the examiner uses affects the interpretation of interaction strengths.

Prey dispersal ability (μ_{prey}) affects the degree to which prey and predators interact within the spatial area. For cases 12, 13, and 14 average predator and initial prey density across the spatial grid, and prey carrying capacity were held constant between simulations. However, prey dispersal ability and the spatial scale of the study (25 or 49 cell grid) were varied. Differences related to predator function response (linear functional response, predator interference, and saturating functional response) were determined. This allowed assessment of the degree to which prey dispersal interacts with predator spatial structure and the scale of the study area to affect interpretation of interaction strengths. Increasing the size of the spatial grid can be interpreted as either an increase in spatial extent or grain of a study area.

For the previously described cases, the spatial grid examined is assumed to be an "island" where the prey and predator populations do not interact with populations outside the spatial area. However, if the study area an examiner chooses is not isolated from the surrounding populations, measured interaction strengths may be misinterpreted. In cases 15 and 16, two spatial grids, 9 and 25 cells, were surrounded by a border of prey zero, one, or two cells wide. Average predator and initial prey density within the 9 or 25 cell study area was held constant between simulations. Interaction strengths were calculated within the 9 or 25 cell study area to determine the effects of ignoring the surrounding area.

Another approach to assess effects of scale is to manipulate the spatial extent of the grid and prey movement in the model system. For prey populations with a high

degree of movement, a larger spatial scale might be necessary to effectively measure interaction strength By holding the number of predator patches constant while increasing the distance between predator patches proportionately to the spatial extent of the grid, the interaction of spatial extent with prey movement can be examined. In case 12 (Tables 1 and 3), predators were confined to 3 boundary cells, 3 spread out cells, 4 boundary cells, 4 spread out cells, 5 spread out cells, or 9 spread out cells on grids of varying spatial extents (Fig. 2). As the spatial extent increases from 25 to 49 cells, the distance between predator cells increases from 3 to 5 cells for predators occupying 3 or 4 boundary cells, 1 to 2 cells for predators occupying 9 spread out cells, and 1 to 3 for predators occupying 3, 4, or 5 spread out cells. For each predator distribution and spatial extent, prey movement was also increased from μ_{prey}=0.0 to 0.8. As the spatial extent of the area is increased, a corresponding increase in prey movement in the model system should be necessary to achieve similar interaction strengths.

CHAPTER 3

RESULTS

In general, spatial variation in predator density affects the four measures of interaction strength (Eqs. 2.1 - 2.4). For all simulations, a uniform distribution of predators in all grid cells gave equivalent results to the case without considering space, as in Berlow et al. (1999). After 40 time steps, most simulations with logistic prey growth were at equilibrium or approaching equilibrium. DI is least informative as the model system moves toward equilibrium since it approaches zero through time. However, relative differences in DI due to predator spatial arrangement are still apparent close to equilibrium. Results for each of the sixteen model scenarios are summarized in Table 4.

Exponential growth

With simple exponential prey growth (Tables 1 and 3; case 1), all four interaction strengths varied over the course of the experiment regardless of initial prey density (Fig. 3). The only exception was DI when predators were uniformly distributed across all grid cells. In this case, DI was constant over the course of the experiment and corresponded to the attack rate coefficient, a. For other prey spatial arrangements, DI weakened (became less negative) over time and was much weaker than in the case of uniformly distributed predators.

At the end of the simulation, all four interaction strengths varied with the spatial structure of the predator (Fig. 4). Interaction strength generally weakened (became less negative) as the proportion of cells to which predators were confined decreased. Both RD and CI depended on initial prey density for all spatial arrangements. Both PI and DI were insensitive to changes in initial prey density regardless of the predator spatial structure (Fig. 4). However, for a particular number of cells with predators, the variability in interaction strengths (coefficient of variation) among different predator distributions (e.g. 4 cells with predators either clumped, spread out, or confined to the spatial grid boundary) was relatively high, but identical for different initial prey densities (Fig. 5). Interaction strengths were typically strongest when predator patches were spread throughout the spatial area (Fig. 6). For predators confined to 3 or 4 cells, interaction strengths were weakest for spatial arrangements where predators were clumped or confined to boundary cells.

Predator movement

With logistic prey growth and movement of both predators and prey (Tables 1 and 3; case 2), all four interaction strengths were variable over time and among predator spatial distributions (Fig. 7). Interaction strength was strongest (most negative) for uniform predator distribution. However, the order of spatial arrangements from least to most negative changed over time, and did not always reflect a decrease in interaction strength as predators were confined to fewer cells. In particular, interaction strengths for 3 or 4 predator patches confined to boundary cells (3 and 4 very spread) did not strengthen as quickly over time as other spatial arrangements. Interaction strengths for

one cell, two cells, and 3 spread cells became increasingly negative over time, eventually exceeding interaction strengths for spatial arrangements that had been stronger early in the simulation.

Over time, predator dispersal from original cell locations led to a uniform distribution across the entire spatial grid. Consequently, over time, all interaction strengths, regardless of initial predator spatial arrangement, approached the interaction strengths for a uniform predator distribution. However, the rate at which each predator spatial arrangement approached a uniform distribution, and consequently the order of spatial arrangements over time, depended on the initial predator distribution.

Variable initial prey density (constant carrying capacity)

With constant carrying capacity, logistic growth, and a linear predator functional response (Tables 1 and 3; case 3), all interaction strengths except DI were variable over time and among predator spatial distributions, but each spatial arrangement approached its own equilibrium after approximately 10 to 20 timesteps for any initial prey density (Figs. 8, 9). When initial prey density was low ($N_0 = 100$), RD, CI, and PI were strongest after 5 to 10 time steps then weakened slightly over time (Fig. 8). DI was also variable, but for all predator spatial arrangements weakened toward zero over time. At equilibrium, all four interaction strengths were insensitive to variability in initial prey density and for predators occupying a particular number of cells, variability among different predator arrangements was relatively small (Fig. 10). All four interaction strengths were strongest (most negative) for uniform predator distribution and decreased as predators were confined to fewer cells.

Modifying the functional response of the predators to a saturating functional response of prey density (Tables 1 and 3; case 4) has marked effects on interaction strength. For all initial prey densities, interaction strengths were variable over time and among predator spatial arrangements (Figs. 11, 12, 13). When initial prey density was low (N_0 =100), the order of spatial arrangements from least to most negative interaction strength changed over time (Fig. 11). With widespread predators (occupying 25 or 9 cells), prey population size early in the simulation was lower than for other predator spatial arrangements, but eventually reached higher carrying capacities (not shown). Consequently, early in the simulation, interaction strengths became less negative as predators were confined to fewer cells, but as the populations approached equilibrium this was no longer true. For higher initial prey densities, when prey were closer to carrying capacity, the order of spatial arrangement was generally the same over time, with a few exceptions (Fig. 12, 13).

At equilibrium, for logistic prey growth with a saturating predator functional response, interaction strengths were insensitive to changes in initial prey density (Fig. 14). The relation of interaction strength to predator spatial arrangement was less clear than the case of a linear functional response. Interaction strength was weakest (least negative) when predators were confined to 1 or 2 cells, or more widely distributed in 9 or 25 cells. At intermediate predator distributions (3, 4, or 5 cells), predator density per cell was high enough to keep overall prey densities lower than that of other spatial arrangements, resulting in stronger interaction strengths. For intermediate numbers of predator patches, interaction strengths were also more variable among different predator distributions within a particular number of predator cells.

Variable initial prey density (variable carrying capacity)

With logistic prey growth, variable carrying capacities, and linear functional response (Tables 1 and 3; case 5), all interaction strengths except DI were variable over time and among predator spatial distributions, but each spatial arrangement quickly approached its own equilibrium regardless of initial prey density (Fig. 15). At equilibrium, all four interaction strengths decreased as predators were confined to fewer grid cells (Fig. 16). RD and CI depended on carrying capacity for all spatial arrangements. However, PI and DI were insensitive to changes in carrying capacity regardless of predator spatial arrangement. For predators occupying a particular number of cells, variability among different spatial arrangements was relatively small.

Modifying the predator functional response to a saturating function of prey density (Tables 1 and 3, case 6) led to variability in the magnitude of interaction strengths among the different spatial arrangements. For all carrying capacities, interaction strengths were variable over time and each spatial arrangement approached its own equilibrium. The order of spatial arrangements from most negative to least negative was generally the same over time, with a few exceptions (Figs. 13 and 17). However, the order of spatial arrangements depended on the prey carrying capacity (Fig. 18).

At equilibrium, all four interaction strengths for logistic prey growth with a saturating predator functional response depended on prey carrying capacity (Fig 18). PI and DI differed from RD and CI in that they emphasized the effects on rare prey or low productivity sites, i.e stronger interaction strengths were skewed toward lower

carrying capacities. However, RD and CI were most sensitive to carrying capacity when predators were confined to less than 20% of the grid cells, when PI and DI were least sensitive (Fig. 19). At low prey density (N_0=K=100), all four interaction strengths weakened (became less negative) as predators were confined to fewer cells. A similar pattern existed for N_0=K=500, but interaction strengths also weakened slightly for widespread predators in 9 or 25 cells. At higher carrying capacities, interaction strengths were stronger at intermediate numbers of predator patches and were more variable among different predator distributions within a particular number of predator cells (Fig. 20). When prey carrying capacity was high and predators occupied 3 or 4 cells, interaction strengths were strongest when predators were spread out in boundary cells (see Fig. 13 for N_0=K=1000; other carrying capacities not shown).

Variable predator density

When average predator density across the spatial grid was variable (Tables 1 and 3; case 8), all four interaction strengths were variable over time, but each spatial arrangement approached its own equilibrium after approximately 10 to 20 time steps. The order of interaction strengths from least to most negative for the different spatial arrangements was the same over time, regardless of predator density. When predator density was low (P=1, 5), RD, CI, and PI were strongest between 5 and 10 time steps then weakened slightly over time (Fig. 21). At higher predator densities, this was true when predators were not uniformly distributed (Fig. 22). Only when predators were uniformly distributed and P>10 did the predator drive the prey extinct.

At equilibrium, all four interaction strengths weakened (became less negative) as predators were confined to fewer cells, regardless of predator density (Fig. 23). When predators were uniformly distributed (proportion of cells with predators was 1), RD, CI, and PI did not depend on predator density, except in cases where prey were driven extinct (P_0>10). DI, on the otherhand, became more negative as predator density increased for uniformly distributed predators. For all other predator spatial arrangements, interaction strengths depended on predator density. For predators occupying a particular number of cells, variability among the different spatial arrangements was relatively low.

With logistic prey growth and predator interference, interaction strengths followed dynamics similar to simulations without predator interference (see Fig. 21). High uniform predator densities, however, did not drive prey extinct. At equilibrium, all four interaction strengths weakened (became less negative) as predators were confined to fewer cells (Fig. 24). Interaction strengths were sensitive to predator density for all predator spatial arrangements, but were least sensitive when predators were confined to only a few cells. For predators occupying a particular number of cells, variability among the different spatial arrangements was relatively low.

Spatial extent and local predator density

Reducing the spatial grid to 9 cells (Tables 1 and 3; case 7) or expanding it to 49 cells (Tables 1 and 3; cases 9, 11) had little effect on interaction strengths for logistic prey growth with or without predator interference, regardless of predator density (Figs. 25, 26, 27). Interaction strengths depended on the proportion of the spatial grid occupied by

the predator. Hence, predators occupying 4 cells on a 9 cell grid (occupying 44% of the spatial area) resulted in similar interaction strengths to predators occupying 9 cells on a 25 cell grid (36% of the spatial area) or 25 cells on a 49 cell grid (51% of the spatial area).

While interaction strengths varied with the proportion of grid cells occupied by predators, the local predator density in a single predator-occupied cell (the total predators in spatial grid divided by the number of cells with predators) was most important in determining interaction strength (see Table 2). High local predator densities occurred when predators were confined to only a few cells. For a particular local predator density, interaction strengths were very similar among different simulations (Figs. 28 and 29). This was true regardless of the number of cells occupied by predators, the average predator density on the entire spatial grid, or the spatial extent of the grid (9, 25, or 49 cells). The only exception was with no predator interference and high uniform predator density when prey were driven to extinction (Fig. 28)

Prey dispersal ability

With logistic prey growth, no predator interference, linear predator functional response, and variable prey dispersal (Tables 1 and 3; case 12) interaction strength dynamics were variable over time and each spatial arrangement approached its own equilibrium (dynamics for different μ_{prey} were qualitatively similar to dynamics in Fig. 8).

At equilibrium, interaction strength weakened as predators were confined to fewer cells for all prey dispersal abilities and both 25 and 49 cell grids (Figs. 30 and 31). When predator density was uniform, i.e the proportion of cells with predators was 1,

prey dispersal ability had no effect on interaction strength. For other spatial arrangements, interaction strength generally strengthened (became more negative) as prey dispersal ability increased although the effect was weak when predators were confined to only 1 or 2 grid cells. However, when predators occupied greater than 30% of the spatial area, interaction strengths were stronger when prey dispersal was low (μ_{prey}=0, 0.1). For a particular number of cells with predators, the variability in interaction strengths among different predator distributions (e.g. 4 cells with predators either clumped, spread out, or confined to the spatial grid boundary) increased as prey dispersal ability increased for both a 25 and 49 cell grid (Figs. 32 and 33). Interaction strengths were strongest when predators were spread throughout the spatial area, rather than clumped in central cells or confined to the boundary (Fig. 34).

When simulations were modified to include predator interference (Tables 1 and 3, case 13), dynamics over time were similar to simulations without predator interference (see Fig. 8). At equilibrium, interaction strengths weakened as predators were confined to fewer cells (Figs. 35 and 36). With predator interference, interaction strengths at equilibrium were not as sensitive to prey dispersal ability as interaction strengths without predator interference. When prey do not move (μ_{prey}=0), interaction strengths were only slightly stronger (more negative) than when prey did move. Additionally, with predator interference, variability among spatial arrangements for a particular number of predator-occupied cells was much lower than variability without predator interference (Figs. 37 and 38).

When predator functional response was a saturating function of prey density (Tables 1 and 3; case 14), interaction strength depended on the dispersal ability of prey.

For all μ_{prey}, the order of spatial arrangements from least to most negative interaction strength changed over time (Figs. 11 and 39). Although early in the simulation, interaction strengths became less negative as predators were confined to fewer cells, as the populations approached equilibrium this was no longer true. At equilibrium, interaction strengths among the different spatial arrangements were most similar when prey dispersal ability was high (Fig. 40). Interaction strengths were strongest when prey dispersal ability was low and predators occupied an intermediate portion of the spatial area. In contrast, when predators were confined to 1 or 2 cells, interaction strengths increased with increasing prey dispersal ability. For a particular number of cells with predators, the variability in interaction strengths among different predator distributions (e g. 4 cells with predators either clumped, spread out, or confined to the spatial grid boundary) was relatively high for intermediate values of prey dispersal (Fig. 41). When predator dispersal was high, interaction strengths were typically weakest when predator patches were spread throughout the spatial area (Fig. 42). For predators confined to 3 or 4 cells, interaction strengths were strongest for spatial arrangements where predators were clumped or confined to boundary cells.

When prey dispersal is high and there is no predator interference, local predator density is a less reliable predictor of interaction strength. When prey dispersal is increased from μ_{prey}=0.2 to μ_{prey}=0.8, there is much more variability in interaction strength for a particular local predator density (compare Fig. 28 to Fig. 43). With predator interference, interaction strength is insensitive to prey dispersal ability and strongly related to local predator density.

Study area surrounded by prey matrix

For two spatial extents, 9 and 25 cells, the grid examined was surrounded by a border of prey zero, one, or two cells wide (Tables 1 and 3; cases 15 and 16). When predators were confined to only a few cells, the presence of a surrounding prey population interacting with the study area had little effect on interaction strength (Fig. 44). When predators were uniformly distributed within the study area, the presence of a surrounding prey matrix resulted in less negative, or weaker, interaction strengths. For the 9 cell study area, there was no difference in interaction strength when the surrounding prey matrix was one or two cells wide.

Interaction of spatial scale and prey dispersal ability

Another approach to assess effects of scale in the model system is to hold constant the number of predator patches but increase the distance between predator patches proportionately to the spatial extent of the grid with a corresponding increase in prey dispersal ability (Tables 1 and 3; case 12). For a particular degree of prey movement, increasing the distance between predator-occupied cells resulted in weaker (less negative) interaction strengths (Fig. 45). However, with a corresponding increase in prey dispersal ability on the 49 cell grid, interaction strength at the larger spatial extent became more negative, approaching that of lower prey dispersal on the smaller spatial grid. This is particularly true when predators are spread throughout the grid (3, 4, or 5 spread out cells). When predators were confined to boundary cells (3, 4, or 9 cells along boundary), even a high degree of prey dispersal did not make up for the increased distance between predator-occupied cells.

CHAPTER 4

DISCUSSION

Effects of spatial structure on interaction strength

The spatial structure of predators generally affected consumer-prey interaction strengths. For exponential or logistic prey growth, linear functional response, with or without predator interference, interaction strengths were strongest when predators were uniformly distributed and weakened as predators were confined to smaller proportions of the spatial area. For these cases, the order of interaction strengths from weakest to strongest among the different spatial arrangements was consistent over the course of the study and at equilibrium . Limiting the distribution of keystone species has been shown empirically to weaken their impact (Estes and Palmisano 1974, Wootton 1995, Prince 1995). The results reported here are consistent with such observations, but additionally indicate that the ordering of interaction strengths does not vary over time.

In contrast, when predator functional response was a saturating function of predator density (Type II, Holling 1958), the order of interaction strengths among different predator arrangements was variable over time, particularly when initial prey density was well below carrying capacity. When initial prey densities were low, widespread predators (occupying 25 or 9 cells) greatly reduced prey populations early in the simulation. Factors such as hunting pressure or disturbance can reduce prey populations to well below carrying capacity. Under such conditions, widespread predators may have much stronger impacts than cases where prey are closer to carrying

capacity. When predators were widespread (occupying 9 or 25 cells), prey populations attained higher average densities than other spatial arrangements as they approached carrying capacity, resulting in weaker interaction strengths. This differs from the case of a linear functional response in that prey are able to attain relatively high densities as long as predator density per cell is relatively low (i.e. predators are widespread) or predators are confined to only a few cells.

With a saturating functional response, the magnitude of interaction strength at equilibrium depended on both the prey carrying capacity and the spatial arrangement of predators. For abundant prey, which could be viewed as high productivity sites, interaction strength was typically strongest for predators confined to an intermediate proportion of the spatial area (neither uniformly distributed or confined to less than 10% of the spatial area). Prey are able to maintain relatively high densities as long as predator density per cell is relatively low or predators are confined to only a few cells. For prey with low carrying capacities, however, uniformly distributed predators had much stronger impacts than more confined predators.

The spatial arrangement of predator patches, i.e. clumped, spread out, or confined to edge cells, had only moderate effects on interaction strength. For most simulations, there was only slight variability among spatial arrangements. Variability was higher for exponential prey growth, saturating functional response, or high prey dispersal. With a linear functional response, predators spread throughout the spatial area tended to have slightly stronger interaction strengths, and variability increased as the dispersal ability of prey increased. With a saturating functional response, variability was highest for intermediate prey dispersal abilities. When prey dispersal was high,

interaction strengths were weakest when predators occupying a particular number of cells were spread throughout the spatial area rather than clumped or confined to boundary cells.

Comparison of interaction strength indices

All four interaction strengths tended to be most negative for uniformly distributed predators over other predator spatial distributions. For exponential or logistic prey growth, linear functional response, with or without predator interference, all four interaction strengths were stronger for uniformly distributed predators, especially when predator density or prey dispersal ability were high. With a Type II predator functional response, the four interaction strengths were skewed toward stronger values for widespread predators (occupying 9 or 25 cells) only when initial prey density was far from carrying capacity and simulations were far from equilibrium.

The four different interaction strengths were affected differently by predator spatial distribution when many prey and predator characteristics were varied. With a Type II functional response and logistic prey growth, PI and DI were stronger for rare prey, or low productivity sites, while RD and CI were stronger for higher prey carrying capacities. However, RD and CI were most sensitive to carrying capacity when predators were confined to less than 20% of the grid cells, when PI and DI were least sensitive. With predator interference and logistic prey growth, for all spatial arrangements, interaction strengths were stronger for rare predators. Without predator interference, RD, CI, and PI were insensitive to average predator density when predators were uniformly distributed and did not drive prey extinct, but were strongest

for rare predators for all other spatial arrangements. DI also emphasized rare predators, but emphasized abundant predators when predators were uniformly distributed.

Prey movement and interaction with predators

Without predator interference and with a linear functional response, high prey dispersal ability led to stronger interaction strengths, except when predators were more widespread (occupying more than 30% of the spatial area). With a Type II functional response, interaction strengths increased with increasing prey dispersal only when predators were confined to a few cells. The relation of prey dispersal ability to predator spatial arrangement likely reflects a shifting balance between prey entering and escaping predator occupied cells. When predators were limited in spatial distribution, high prey dispersal likely increased the number of prey entering predator occupied cells and the predator population was able to interact with a greater fraction of the prey population. When predators were widespread, however, high prey dispersal ability allowed a greater fraction of prey to escape predator occupied cells. A saturating predator functional response may magnify this effect at intermediate predator spatial arrangements as where prey entering predator-occupied cells fail to reach high enough densities to weaken the capture ability of predators. High prey dispersal from predator-dense patches has been shown to weaken predator-prey interaction strengths in nature (Fagan and Hurd 1994).

In contrast, when predators interfered with each others ability to capture prey, interaction strengths were insensitive to prey dispersal ability for all predator spatial distributions, except for being slightly stronger when prey did not disperse. Predator

interference weakened the per capita capture rate of predators. Consequently, even when prey dispersal was high and a greater fraction of prey were entering or escaping predator occupied cells, there was little effect on interaction strength.

Spatial scale

Spatial scale of the study area had little effect on interaction strength when interpreted properly When comparing areas of different spatial extents but similar predator densities, the most important determinant of interaction strength is the fraction of the study area occupied by predators. Hence, an empirical study comparing areas of different sizes but equivalent predator densities will likely result in different interaction strengths if the fraction of the study area occupied by predators differs among the study sites.

Prey dispersal can interact with spatial scale, particularly if there is low predator interference, which could occur at low predator densities. Furthermore, the spatial extent an examiner chooses should reflect the dispersal abilities of the interacting populations. Large spatial extents may underestimate the interaction strengths for populations with low dispersal.

The most important determinant of interaction strength was the local predator density. An empirical approach that compares large study sites with different predator densities and spatial distributions may find similar interaction strengths if the local predator densities are similar. Within a study site, a predator population may be widespread or limited in distribution. However, when there are few prey or predator movements, the actual consumer-prey interaction is confined to a local area.

Consequently, when possible, a field ecologist might be best served by taking a fine-grained approach, estimating predator and prey density only in the local area in which predator and prey interact. However, the results here show that local density measures are less accurate predictors of interaction strength when prey dispersal is high. Empirical studies indicate that local density measures may underestimate the impacts of species mobility (Navarrete and Menge 1996).

When the local extent of predator-prey interaction cannot be assessed, or prey movement is high, care must be taken when choosing study sites. Study areas with similar predator densities may have different interaction strengths depending on the spatial distribution of the predator. Assuming uniform predator densities or neglecting the importance of space can lead to underestimates of interaction strength. Furthermore, if predators are interacting with prey outside the study area, interaction strengths may be underestimated.

Summary of results

The consumer-prey interaction explored here emphasizes the importance of recognizing spatial structure and scale when interpreting interaction strengths. The simulations developed here showed that interaction strength is affected by spatial structure in the following ways:

1) In general, interaction strength is strongest when predators are uniformly distributed and weakens as predators are confined to smaller proportions of the spatial area, and this order of spatial arrangements is consistent over time. This is not necessarily true, however, for a saturating predator functional response.

2) With a saturating functional response, interaction strengths for different predator spatial distributions depend on the length of the experiment, initial prey density, and rarity of prey. Widespread predators have stronger interaction strengths than more confined predators only when initial prey density is well below carrying capacity, or prey carrying capacity is low. Hence widespread predators may have unexpectedly strong effects when factors such as hunting pressure or disturbances reduce prey populations to well below carrying capacity. Furthermore, an increase in productivity that increases prey carrying capacity can weaken the impact of uniformly distributed predators.

3) The spatial arrangement of predator patches, i.e. clumped, spread out, or confined to edge cells, has only moderate effects on interaction strength, except when predator functional response is saturating or prey dispersal is high. Interaction strengths are generally stronger when predators are spread throughout the spatial area, unless prey reach densities where they interfere with the ability of predators to capture prey.

4) Movement of predators allows predators to interact with prey populations in a wider area, and consequently results in stronger interaction strengths. Interation strength also depends on the degree of prey movement, reflecting a balance between prey entering predator-occupied cells when predators are limited in distribution, escaping predator-occupied cells when predators are widespread, and reaching high densities capable of reducing the capture ability of predators

Each of the four interaction strength indices have certain biases and must be interpreted accordingly. Slight differences in prey or predator abundance between

study sites can result in large differences in interaction strength, but this depends on which interaction strength index is measured, the length of the experiment, and the spatial arrangement of the predators:

1) All four interaction strengths, for any particular predator spatial arrangement, were variable over time. Although the relative order of interaction strengths among different predator spatial distributions was generally consistent over time, the magnitude of interaction strengths was variable. Consequently, interpretation of experimental results should account for the length of the experiment. Berlow et al. (1999) previously recommended DI be used when comparing short-term results. RD, CI, and PI are more appropriate for long-term experiments. When comparing different predator spatial distributions, however, qualitative differences in RD, CI, PI, or DI are generally comparable between short-term and long-term experiments, except when the predator functional response is a saturating function of prey density.

2) With a saturating functional response, results presented here agree with Berlow et al. (1999) that PI and DI emphasize rare prey. On the other hand, RD and CI are stronger for higher prey carrying capacities. However, the degree to which carrying capacity affects each interaction strength depends on the spatial structure of predators. RD and CI are most sensitive to carrying capacity when predators are confined to only a few cells, while the opposite is true for PI and DI. Therefore, when comparing experimental results, investigators should be aware of both prey abundance and predator spatial structure, regardless of the interaction strength index chosen.

3) Without predator interference, as in Berlow et al. (1999) DI emphasizes abundant predators while RD, CI, and PI are insensitive to average predator density

when predators are uniformly distributed and do not drive prey extinct. However, for all other predator spatial distributions, all four interaction strength indices are stronger for rare prey. Hence, comparison of experimental results must account for both rarity of prey and predator spatial structure.

The spatial extent and resolution an examiner chooses can also impact how interaction strengths are interpreted:

1) The fraction of area occupied by a predator determines interaction strength when comparing areas of different spatial extents but similar predator densities.

2) The spatial extent examined should be large enough to account for the degree of prey and predator movement, otherwise interaction strengths may be overestimated.

3) The most reliable estimate of interaction strength is found by measuring prey and predator populations in the local area in which they interact, rather than taking an average over a large spatial area. Local interaction strength is less accurate, however, with a high degree of prey movement.

Conclusions

A reliable and accurate interpretation of interaction strengths cannot ignore spatial structure and scale. Factors such as variability in productivity, periodic disturbances, the presence of predators or strong competitors, social interactions among predators, or the spatial variability in habitat conditions can all limit the distribution of consumers (Estes and Palmisano 1974, Gilbert 1980, Paine 1992, Creed 1994, Wootton 1995), and consequently, weaken consumer-prey interaction strengths. The degree to which interaction strengths are reduced, however, depends on the ability of the predator

to capture prey, the prey density, and the length of the experiment. A high degree of prey movement can also weaken interaction strengths by allowing prey to escape large predator occupied regions. Short-term empirical studies of interaction strength may underestimate the potential long-term effects of the predator or prey movement. Short-term experiments may also overestimate effects of widespread predators, particularly when high prey densities interfere with prey capture rate.

Community-wide effects of spatial structure and scale are difficult to predict from the consumer prey-interaction examined here. Consumer-prey interaction strengths depended on combined effects of prey mobility and predator spatial distribution. For larger communities, the strength of a keystone's impact depends on the number of species who depend on it directly as well as through indirect links (Yodzis 1988, 1996, Abrams et al. 1996, Jones et al. 1994). Consequently, the spatial structure of all interacting species within a community may affect the impact of a keystone species. The impacts of keystone modifiers, mutualists, and resources also depend on the spatial structure of species (Gilbert 1980, Jones et al. 1994). Unlike keystone predators, however, keystone mutualists may be more likely to have strong impacts when they are patchily distributed (Fleming 1985, Gautier-Hion and Michaloud 1989).

The ability to accurately measure and interpret interaction strengths in empirical studies, as well as the ability to detect keystone species in natural communities, clearly depends on the spatial structure of species involved, as well as the spatial and temporal extent and resolution of the study. Comparing the impacts of strong interactors among different communities can only be accurately accomplished with knowledge of the

spatial structure and mobility of species in each community. Accurate measurement and interpretation of interaction strengths also depends on the spatial extent and resolution used by the examiner. Empirical approaches should include an assessment of the local region in which the consumer and prey interact. Neglecting the effects of space can lead to underestimates of interaction strength, and possible mis-identification of keystone species.

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APPENDICES

APPENDIX A

TABLE 1. Parameter and variable values for the cases explored in the predator-prey simulations (see Eq. 2.5). For all simulations r=0.5 and a=0.05 Variables and parameters are as follows: r, intrinsic prey growth rate; a, predator attack rate; μ_{prey}, prey dispersal ability; $\mu_{predator}$, predator dispersal ability; N_0, average initial prey density; K, prey carrying capacity; P, average initial predator density; $c_N>0$, saturating functional response; $c_P>0$, predator interference.

Case	Grid Size	μ_{prey}	$\mu_{predator}$	N_0	K	P_0	c_N	c_P
Exponential prey growth								
1	25	0.2	0	100, 500, 1000, 1500, 2000	N/A	5	0	0
Predator movement								
2	25	0.2	0.2	100	1000	5	0	0
Varying initial prey density, without and with saturating functional response								
3	25	0.2	0	100, 500, 1000, 1500, 2000	1000	5	0	0
4	25	0.2	0	100, 500, 1000, 1500, 2000	1000	5	0.005	0
Varying prey carrying capacity, without and with saturating functional response								
5	25	0.2	0	100, 500, 1000, 1500, 2000	= N_0	5	0	0
6	25	0.2	0	100, 500, 1000, 1500, 2000	= N_0	5	0.005	0
Varying predator density, for various spatial extents, without predator interference								
7	9	0.2	0	100	1000	1, 5, 10, 15, 20	0	0
8	25	0.2	0	100	1000	1, 5, 10, 15, 20	0	0
9	49	0.2	0	100	1000	1, 5, 10, 15, 20	0	0
Varying predator density, for various spatial extents, with predator interference								
10	25	0.2	0	100	1000	1, 5, 10, 15, 20	0	0.1
11	49	0.2	0	100	1000	1, 5, 10, 15, 20	0	0.1

TABLE 1 (continued)

Case	Grid Size	μ_{prey}	$\mu_{predator}$	N_0	K	P	c_N	c_P
Varying prey dispersal, for various spatial extents, with and without predator interference, saturating functional response								
12	25, 49	0, 0.1, 0.2, 0.4, 0.6, 0.8	0	100	1000	5	0	0
13	25, 49	0, 0.1, 0.2, 0.4, 0 6, 0 8	0	100	1000	5	0	0.1
14	25,	0, 0.1, 0.2, 0.4, 0.6, 0.8	0	100	1000	5	0.005	0
Varying surrounding prey matrix								
15	9, 25, 49	0.2	0	100	1000	5	0	0
16	25, 49	0.2	0	100	1000	5	0	0

TABLE 2. Local predator densities (total number of predators in grid/ number of cells with predators) for given average predator densities and spatial extents.

Average predator density	Cells with predators	Local predator density: Grid size 9	Grid size 25	Grid size 49
1	1	9 0	25.0	49.0
	2	4.5	12 5	24.5
	3	3 0	8.3	16.3
	4	2.3	6.3	12.3
	5	1 8	5.0	9.8
	9	1.0	2.8	5.4
	25		1 0	2 0
	49			1.0
5	1	45 0	125.0	245.0
	2	22.5	62 5	122.5
	3	15 0	41.7	81.7
	4	11.3	31.3	61.3
	5	9.0	25.0	49.0
	9	5.0	13 9	27.2
	25		5.0	9.8
	49			5.0
10	1	90 0	250.0	490.0
	2	45.0	125.0	245.0
	3	30.0	83.3	163.3
	4	22.5	62 5	122 5
	5	18.0	50.0	98 0
	9	10.0	27 8	54.4
	25		10.0	19.6
	49			10 0
15	1	135 0	375 0	735 0
	2	67.5	187.5	367.5
	3	45.0	125.0	245.0
	4	33.8	93.8	183.8
	5	27.0	75.0	147.0
	9	15.0	41.7	81.7
	25		15.0	29.4
	49			15.0
20	1	180.0	500 0	980.0
	2	90.0	250.0	490.0
	3	60 0	166 7	326.7
	4	45.0	125.0	245.0
	5	36 0	100.0	196.0
	9	20.0	55.6	108.9
	25		20.0	39.2
	49			20 0

TABLE 3. Summary of sixteen model scenarios examined and objective of each. Parameter and variable values for each case are given in Table 1.

Model Scenario		Assessed ..
Exponential growth	Case 1	Effects of predator spatial distribution on interaction strength with no prey self-limitation
Predator movement	Case 2	Effects of predator spatial distribution on interaction strength with predator movement
Variable initial prey density (constant carrying capacity)	Case 3, Case 4	Effects of predator spatial distribution on interaction strength with variable initial prey density for different predator functional responses (linear or saturating)
Variable initial prey density (variable carrying capacity)	Case 5, Case 6	Effects of predator spatial distribution on interaction strength with variable prey carrying capacity for different predator functional responses (linear or saturating)
Variable predator density	Case 8, Case 10	Effects of predator spatial distribution on interaction strength with variable predator density, with or without predator interference
Spatial extent and local predator density	Case 7, Case 8, Case 9	Effects of spatial extent (grid size) on interaction strength with variable predator density and no predator interference
	Case 10, Case 11	Effects of spatial extent (grid size) on interaction strength with variable predator density and predator interference
Prey dispersal ability	Case 12, Case 13, Case 14	Effects of prey dispersal ability and predator spatial distribution on interaction strength for different predator functional responses (linear, saturating, or predator interference)
Study area surrounded by prey matrix	Case 15, Case 16	Effects of prey outside study area interacting with populations inside study area on interaction strength for different spatial extents (grid sizes)
Interaction of spatial scale and prey dispersal ability	Case 12	Interaction of spatial extent with degree of prey movement when measuring interaction strengths

TABLE 4. Summary of results from each of the sixteen model scenarios (as described in Tables 1 and 3).

Model Scenario	RD	CI	PI	DI
Variable initial prey density				
Exponential growth (case 1)	Weakened as predators confined to fewer patches; Depends on initial prey density	Weakened as predators confined to fewer patches; Depends on initial prey density	Weakened as predators confined to fewer patches; Robust at equilibrium to initial prey density.	Weakened as predators confined to fewer patches; Robust at equilibrium to initial prey density.
Linear F. R (case 3)	Weakened as predators confined to fewer patches; Robust at equilibrium to initial prey density.	Weakened as predators confined to fewer patches; Robust at equilibrium to initial prey density.	Weakened as predators confined to fewer patches; Robust at equilibrium to initial prey density.	Weakened as predators confined to fewer patches; Robust at equilibrium to initial prey density.
Saturating F. R. (case 4)	Strongest at equilibrium for predators confined to 3-5 cells, but order of spatial arrangements changed over time, Robust at equilibrium to initial prey density.	Strongest at equilibrium for predators confined to 3-5 cells, but order of spatial arrangements changed over time; Robust at equilibrium to initial prey density.	Strongest at equilibrium for predators confined to 3-5 cells, but order of spatial arrangements changed over time, Robust at equilibrium to initial prey density.	Strongest at equilibrium for predators confined to 3-5 cells, but order of spatial arrangements changed over time; Robust at equilibrium to initial prey density
Variable prey carrying capacity				
Linear F. R. (case 5)	Weakened as predators confined to fewer patches; Strongest for abundant prey.	Weakened as predators confined to fewer patches, Strongest for abundant prey.	Weakened as predators confined to fewer patches; Robust at equilibrium to prey carrying capacity.	Weakened as predators confined to fewer patches, Robust at equilibrium to prey carrying capacity
Saturating F. R. (case 6)	For low K, weakened as predators confined to fewer cells; Strongest for abundant prey at equilibrium, particularly when predators confined to few cells.	For low K, weakened as predators confined to fewer cells; Strongest for abundant prey at equilibrium, particularly when predators confined to few cells.	For low K, weakened as predators confined to fewer cells; Strongest for rare prey at equilibrium, particularly when predators more widespread.	For low K, weakened as predators confined to fewer cells, Strongest for rare prey at equilibrium, particularly when predators more widespread.

TABLE 4 (continued)

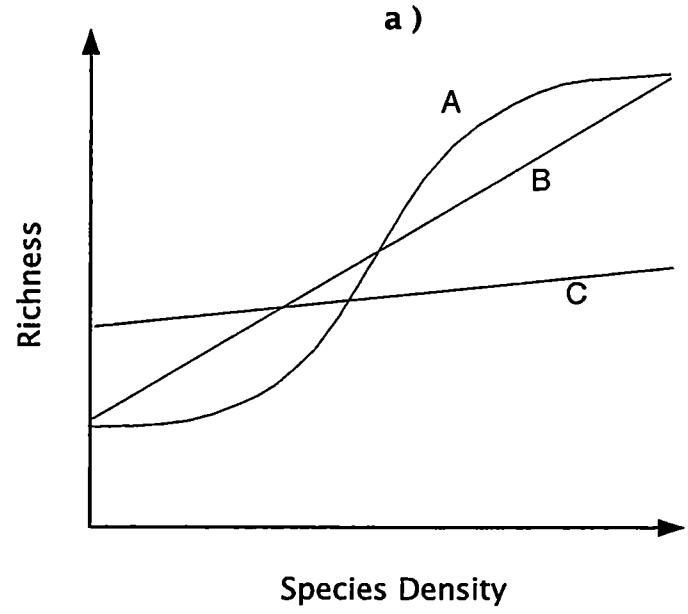
Model Scenario	RD	CI	PI	DI
Predator movement (case 2)				
	Each spatial arrangement approached uniform predator distribution over time	Each spatial arrangement approached uniform predator distribution over time.	Each spatial arrangement approached uniform predator distribution over time.	Each spatial arrangement approached uniform predator distribution over time.
Variable predator density				
No predator interference (case 8)	Weakened as predators confined to fewer cells; Strongest for rare predators at equilibrium, except when predators uniformly distributed.	Weakened as predators confined to fewer cells; Strongest for rare predators at equilibrium, except when predators uniformly distributed	Weakened as predators confined to fewer cells; Strongest for rare predators at equilibrium, except when predators uniformly distributed	Weakened as predators confined to fewer cells, Strongest for rare predators at equilibrium, except when predators uniformly distributed emphasized abundant predators
Predator interference (case 9)	Weakened as predators confined to fewer cells; Strongest for rare predators at equilibrium for all spatial arrangements.	Weakened as predators confined to fewer cells; Strongest for rare predators at equilibrium for all spatial arrangements.	Weakened as predators confined to fewer cells; Strongest for rare predators at equilibrium for all spatial arrangements.	Weakened as predators confined to fewer cells; Strongest for rare predators at equilibrium for all spatial arrangements.
Variable spatial extent (grid size)				
No predator interference (cases 7, 8, 9)	Robust to grid size when measuring local predator density.	Robust to grid size when measuring local predator density.	Robust to grid size when measuring local predator density	Robust to grid size when measuring local predator density.
Predator interference (cases 10, 11)	Robust to grid size when measuring local predator density.	Robust to grid size when measuring local predator density.	Robust to grid size when measuring local predator density.	Robust to grid size when measuring local predator density.

TABLE 4 (continued)

Model Scenario	RD	CI	PI	DI
Variable prey dispersal ability				
Linear F. R (case 12)	Emphasizes higher prey dispersal abilities at equilibrium, except when predators more widespread.	Emphasizes higher prey dispersal abilities at equilibrium, except when predators more widespread	Emphasizes higher prey dispersal abilities at equilibrium, except when predators more widespread.	Emphasizes higher prey dispersal abilities at equilibrium, except when predators more widespread
Predator interference (case 13)	Robust to prey dispersal ability at equilibrium when predators not widespread, except for slight emphasis on non-dispersing prey.	Robust to prey dispersal ability at equilibrium when predators not widespread, except for slight emphasis on non-dispersing prey.	Robust to prey dispersal ability at equilibrium when predators not widespread, except for slight emphasis on non-dispersing prey.	Robust to prey dispersal ability at equilibrium when predators not widespread, except for slight emphasis on non-dispersing prey.
Saturating F. R (case 14)	Strongest at equilibrium when prey dispersal ability low and predators occupied intermediate number of cells, but order of spatial arrangements changed over time; Strengthened with prey dispersal ability when predators confined to 1 or 2 cells,	Strongest at equilibrium when prey dispersal ability low and predators occupied intermediate number of cells, but order of spatial arrangements changed over time; Strengthened with prey dispersal ability when predators confined to 1 or 2 cells;	Strongest at equilibrium when prey dispersal ability low and predators occupied intermediate number of cells, but order of spatial arrangements changed over time; Strengthened with prey dispersal ability when predators confined to 1 or 2 cells;	Strongest at equilibrium when prey dispersal ability low and predators occupied intermediate number of cells, but order of spatial arrangements changed over time; Strengthened with prey dispersal ability when predators confined to 1 or 2 cells;
Prey surrounding study area (cases 15, 16)				
	Strongest for study area populations not surrounded by interacting prey, particularly when predators widespread.	Strongest for study area populations not surrounded by interacting prey, particularly when predators widespread.	Strongest for study area populations not surrounded by interacting prey, particularly when predators widespread.	Strongest for study area populations not surrounded by interacting prey, particularly when predators widespread.

APPENDIX B

FIGURE 1. Hypothetical graphs of how the impact of a keystone species may change with the density of the keystone species. a) gives the change in a community trait, here species richness, as a function of keystone density, and b) gives the change in community importance as a function of keystone density (CI=[d(trait)/dp]/trait where p is the proportional abundance of the keystone; Eq. 1.1). Keystone species would have a CI value greater than 1. Line *A* represents a keystone whose impact depends on a threshold density separating small and weak effects. Line *B* represents a keystone whose community importance decreases with density as one over the ecosystem trait. Line C represents a species which is not a keystone (impact on the community is weak). Here, species *A* and *B* have similar effects on community richness (and the same CI value) when presence at typical density and absence are compared. At intermediate densities, their effects on the community are quite different.


a)
A
B
C
Richness
Species Density

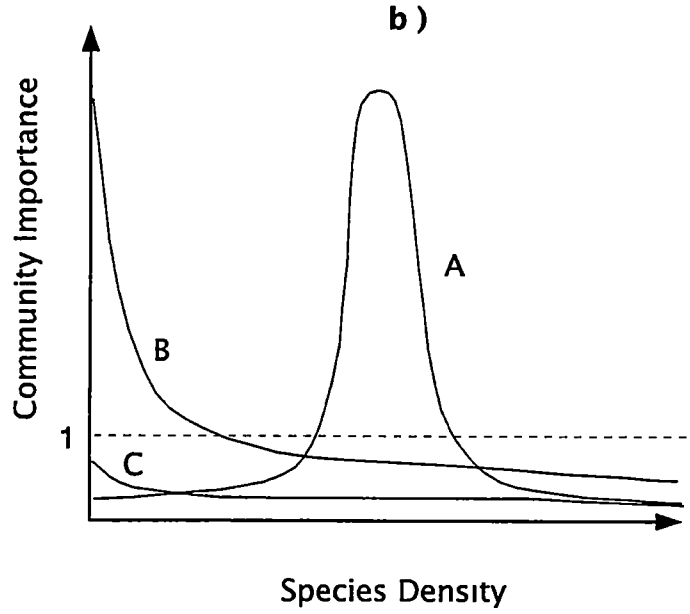

b)
A
B
C
1
Community Importance
Species Density

FIGURE 2. Spatial arrangement of predators for a 25 cell grid (a-o), 9 cell grid (a, b, c, d, e, g, h, l), and 49 cell grid (a-t). Shaded squares indicate predator-occupied cells. Boundary of the 9 cell grid is indicated by the dashed line. Boundary of the 25 cell grid is indicated by the thick black line.

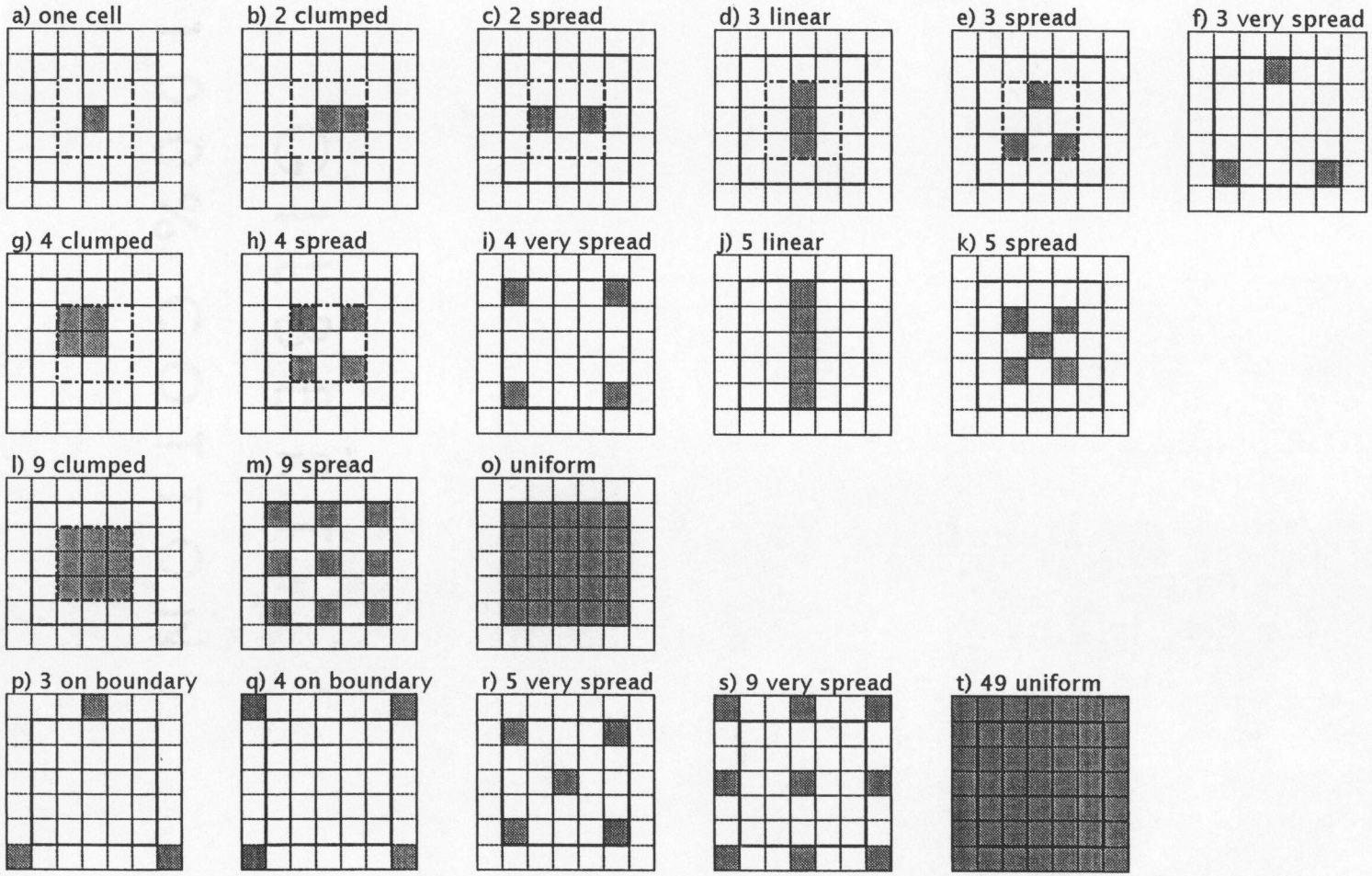


FIGURE 3. Temporal trajectories of the per capita interaction strength for each of the different predator spatial arrangements (Fig. 2) on a 25 cell grid, as measured by the different indices, estimated from simulations with vs. without predators, for case 1 (Table 1), where prey growth was exponential, initial average prey density (N_0) was 100. Average predator density (P_0) and prey dispersal ability (μ_{prey}) were held constant across all runs. Temporal trajectories for initial average prey densities 500, 1000, 1500, and 2000 were qualitatively similar to initial prey density 100, and are not shown. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different predator spatial arrangements; some lines may overlap where interaction strengths were similar.

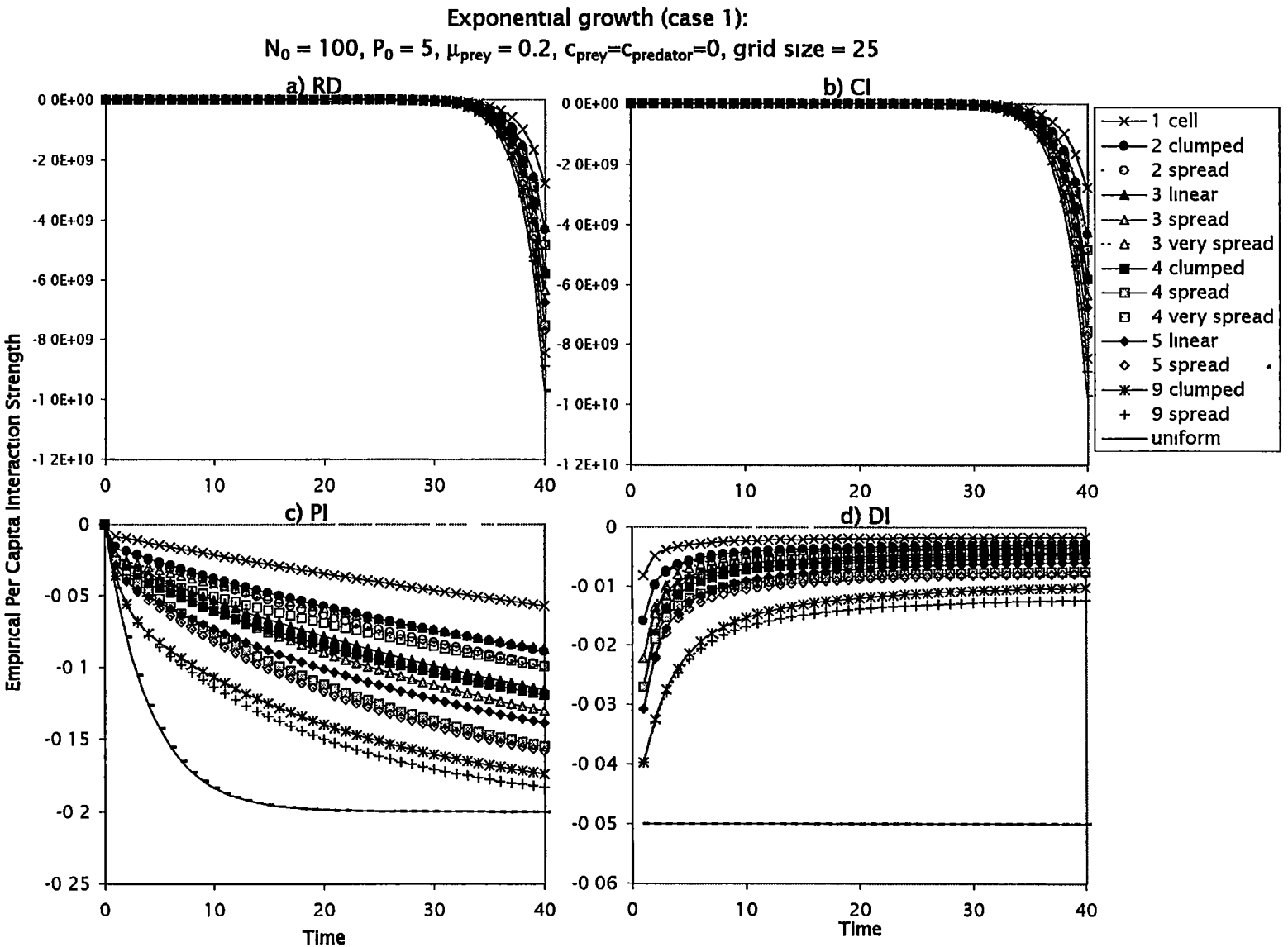

Exponential growth (case 1):
N0 = 100, P0 = 5, μprey = 0.2, cprey=cpredator=0, grid size = 25
a) RD
b) CI
c) PI
d) DI
Empirical Per Capita Interaction Strength
Time
Time
0 0E+00
-2 0E+09
-4 0E+09
-6 0E+09
-8 0E+09
-1 0E+10
-1 2E+10
0
-0 05
-0 1
-0 15
-0 2
-0 25
-0 01
-0 02
-0 03
-0 04
-0 05
-0 06
0
10
20
30
40
1 cell
2 clumped
2 spread
3 linear
3 spread
3 very spread
4 clumped
4 spread
4 very spread
5 linear
5 spread
9 clumped
9 spread
uniform

FIGURE 4. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 25 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 1 (Table 1), where prey growth was exponential, initial average prey density (N_0) ranged from 100 to 2000, and average predator density (P_0) and prey dispersal ability (μ_{prey}) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

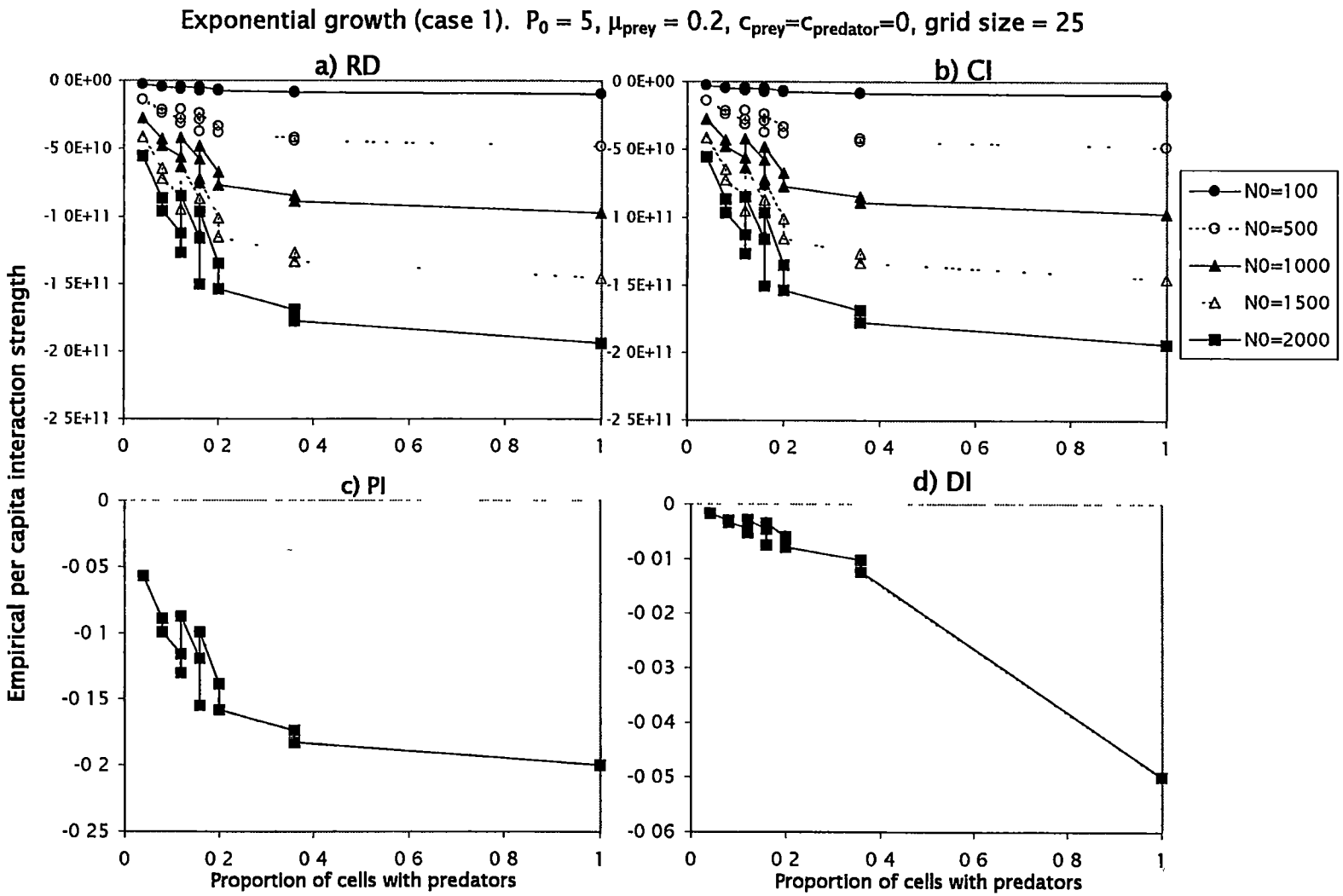

Exponential growth (case 1). P_0 = 5, μ_{prey} = 0.2, c_{prey}=$c_{predator}$=0, grid size = 25
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Proportion of cells with predators
Proportion of cells with predators
N0=100
N0=500
N0=1000
N0=1500
N0=2000

FIGURE 5. Relation of initial prey density (N_0) with exponential prey growth (Table 1; case 1) to the coefficient of variation (CV) for the raw difference (RD) among different predator spatial distributions (linear, clumped, spread, and very spread) for a particular number of cells with predators. Each of the five symbols gives the CV among the following predator distributions (see Fig. 2): i) 2 clumped, spread; ii) 3 linear, spread, very spread; iii) 4 clumped, spread, very spread; iv) 5 linear, spread; and v) 9 clumped, spread. Patterns for the coefficient of variation in CI, PI, and DI were qualitatively similar to that of RD.

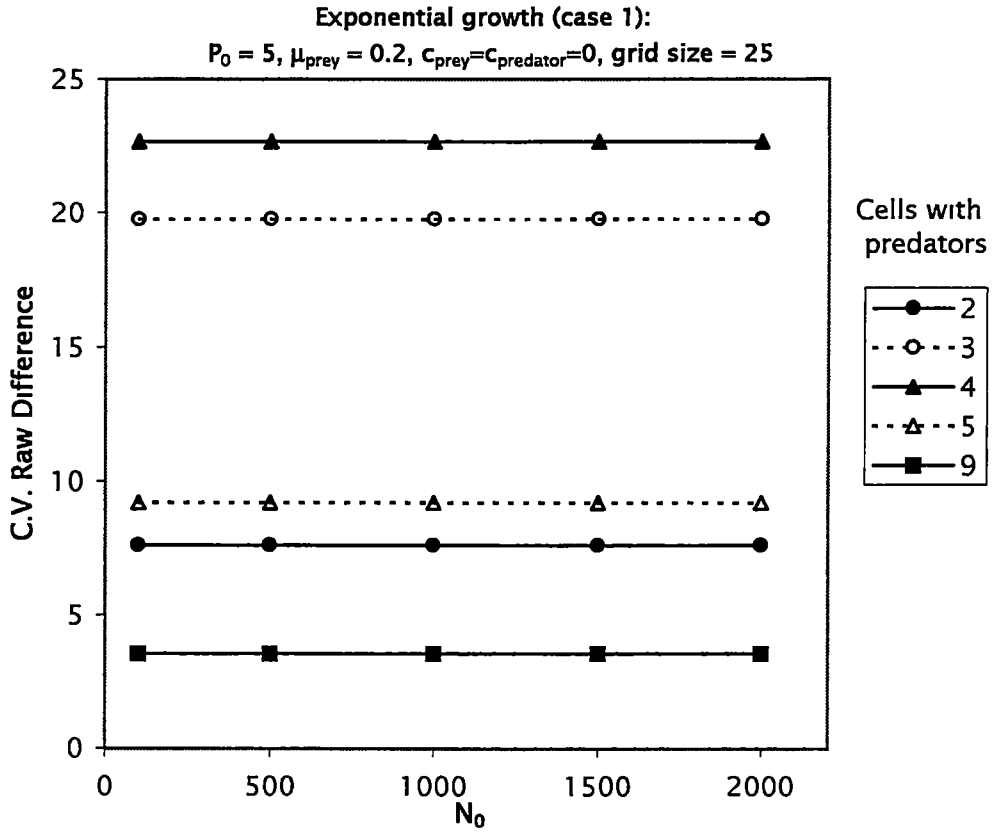


FIGURE 6. Average raw difference (RD) among different initial prey densities (N_0) for each of the predator distributions and number of cells occupied by predators (Fig. 2) where prey growth was exponential (case 1) and predator functional response was linear. Patterns among predator distributions for RD were similar to those for CI, PI, and DI.

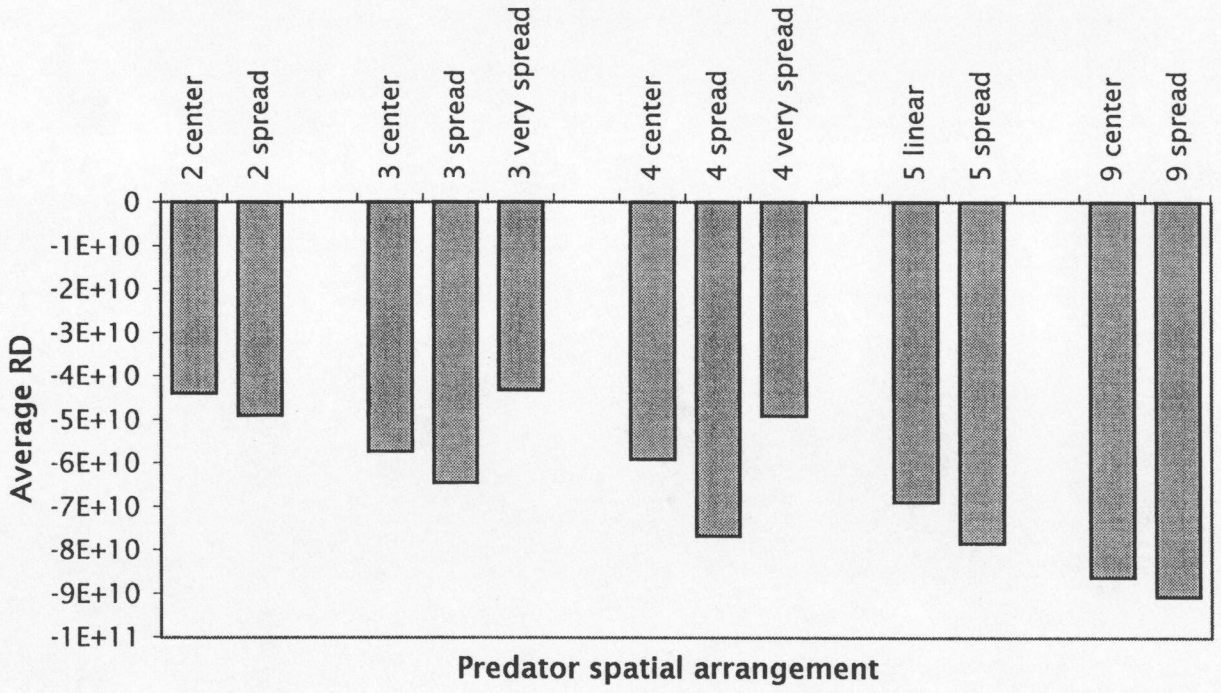


FIGURE 7. Temporal trajectories of the per capita interaction strength for each of the different predator spatial arrangements (Fig. 2) on a 25 cell grid, as measured by the different indices, estimated from simulations with vs. without predators, for case 2 (Table 1), where predator movement was allowed ($\mu_{predator}$=0.2). Logistic prey growth, linear predator functional response, initial average prey density (N_0), prey carrying capacity (K), average predator density (P_0), and prey dispersal ability (μ_{prey}) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different predator spatial arrangements; some lines may overlap where interaction strengths were similar.

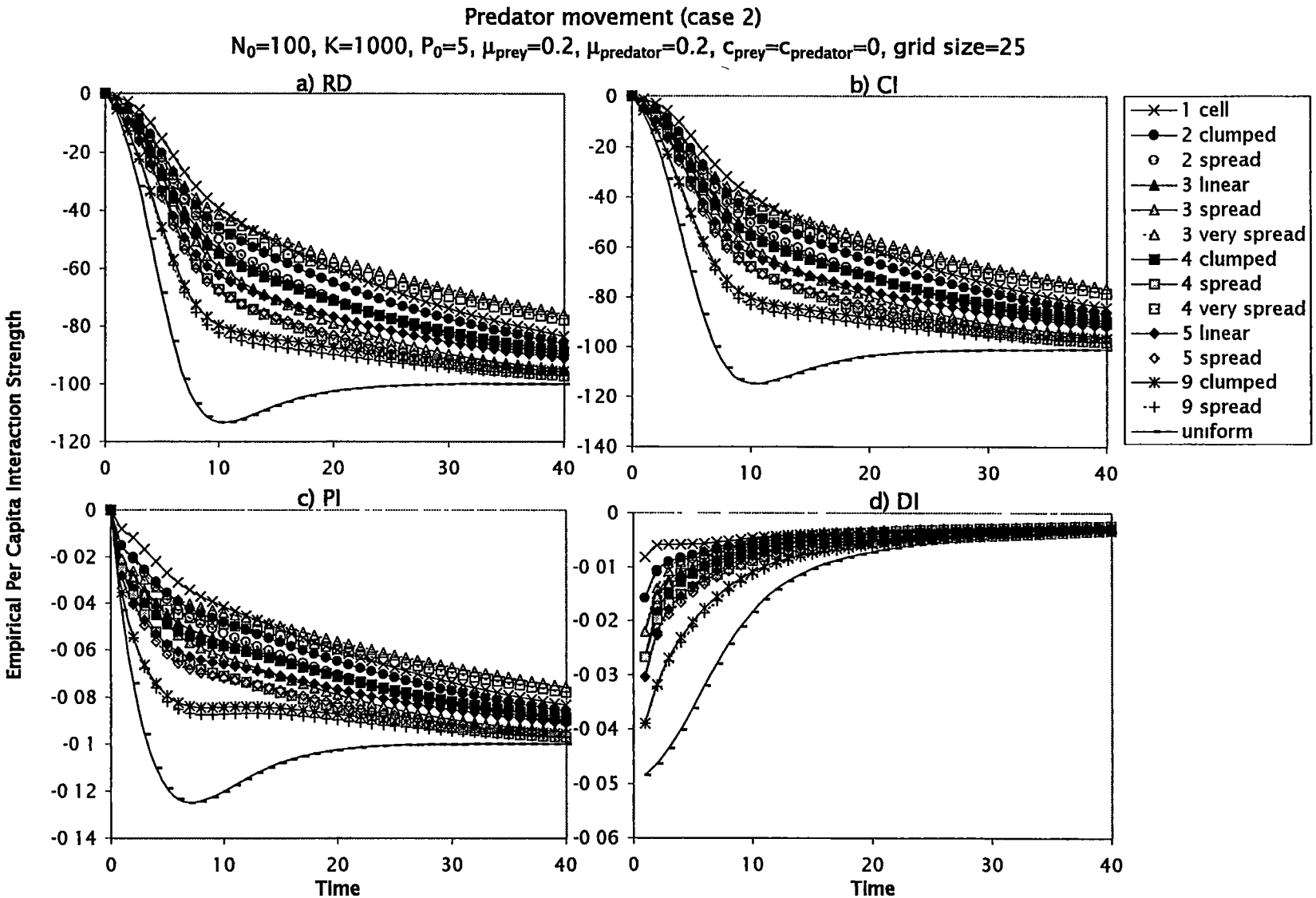

Predator movement (case 2)
N0=100, K=1000, P0=5, μprey=0.2, μpredator=0.2, cprey=cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical Per Capita Interaction Strength
Time
Time
1 cell
2 clumped
2 spread
3 linear
3 spread
3 very spread
4 clumped
4 spread
4 very spread
5 linear
5 spread
9 clumped
9 spread
uniform

FIGURE 8. Temporal trajectories of the per capita interaction strength for each of the different predator spatial arrangements (Fig 2) on a 25 cell grid, as measured by the different indices, estimated from simulations with vs. without predators, for case 3 (Table 1), where prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$), and initial average prey density (N_0) was 100. Average predator density (P_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different predator spatial arrangements; some lines may overlap where interaction strengths were similar.

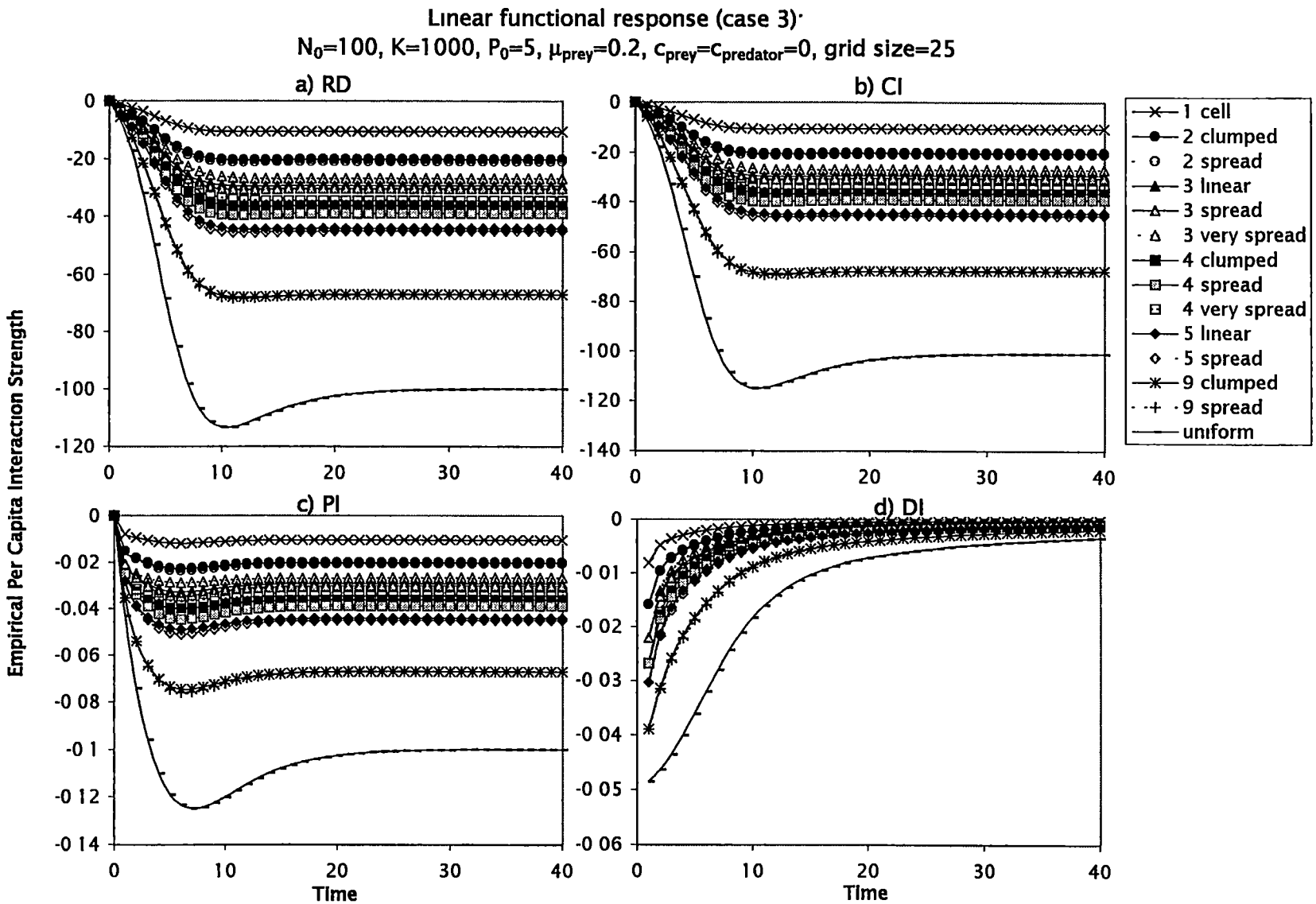

Linear functional response (case 3)·
N0=100, K=1000, P0=5, μprey=0.2, cprey=cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical Per Capita Interaction Strength
Time
Time
1 cell
2 clumped
2 spread
3 linear
3 spread
3 very spread
4 clumped
4 spread
4 very spread
5 linear
5 spread
9 clumped
9 spread
uniform

FIGURE 9. Temporal trajectories of the per capita interaction strength for each of the different predator spatial arrangements (Fig. 2) on a 25 cell grid, as measured by the different indices, estimated from simulations with vs. without predators, for case 3 (Table 1), where prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$), and initial average prey density (N_0) was 2000. Average predator density (P_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. Temporal trajectories for initial average prey densities 500, 1000, and 1500 were qualitatively similar to initial prey density 2000, and are not shown. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different predator spatial arrangements; some lines may overlap where interaction strengths were similar.

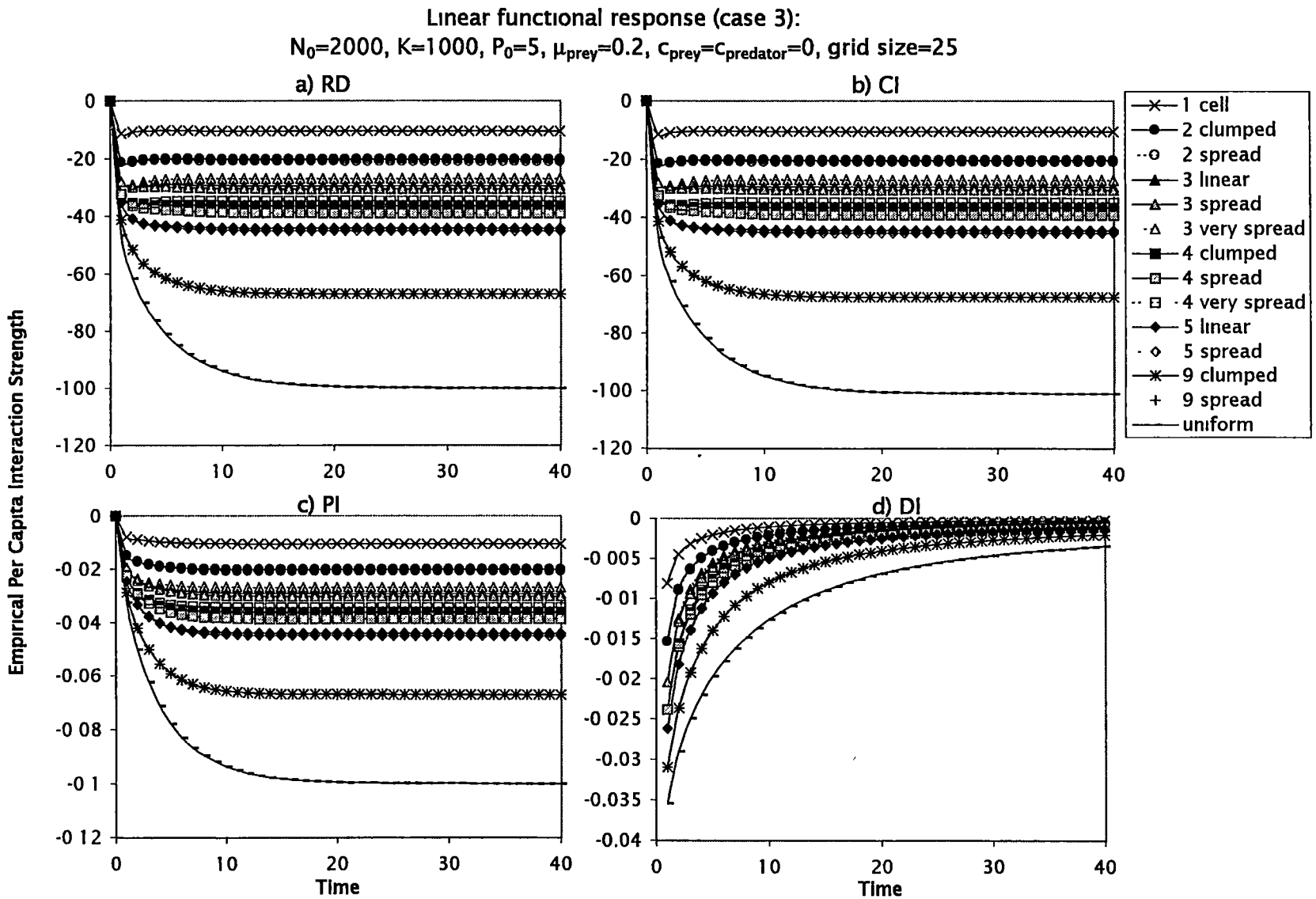

Linear functional response (case 3):
N0=2000, K=1000, P0=5, μprey=0.2, cprey=cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical Per Capita Interaction Strength
Time
Time
1 cell
2 clumped
2 spread
3 linear
3 spread
3 very spread
4 clumped
4 spread
4 very spread
5 linear
5 spread
9 clumped
9 spread
uniform

FIGURE 10. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 25 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 3 (Table 1), where prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$), initial average prey density (N_0) ranged from 100 to 2000, and average predator density (P_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

Linear functional response, constant carrying capacity (case 3):
K=1000, P_0=5, μ_{prey}=0.2, c_{prey}=$c_{predator}$=0, grid size=25

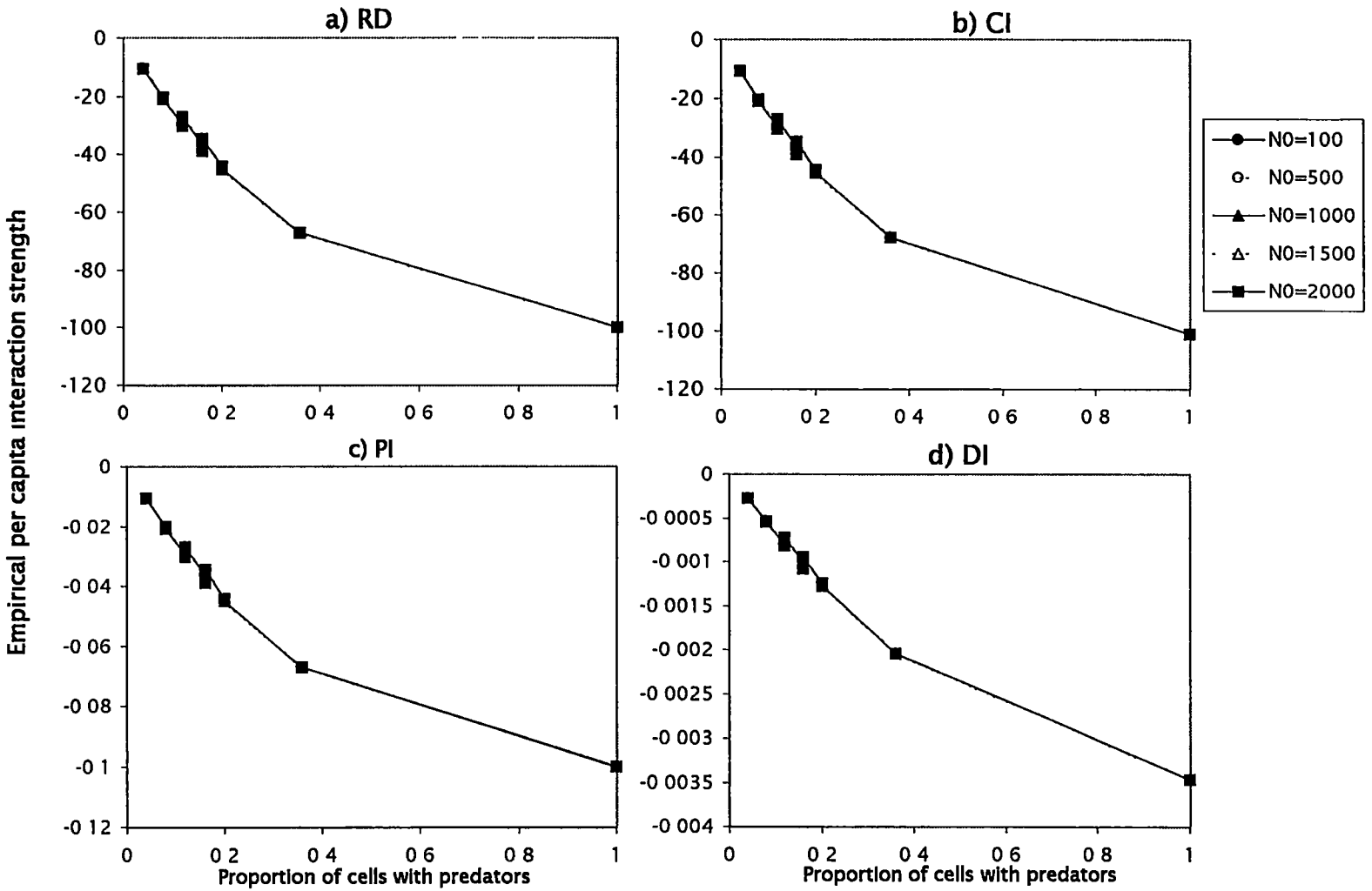


FIGURE 11. Temporal trajectories of the per capita interaction strength for each of the different predator spatial arrangements (Fig. 2) on a 25 cell grid, as measured by the different indices, estimated from simulations with vs. without predators, for case 4 (Table 1), where predator functional response was a saturating function of prey density (c_{prey}=0.005), prey growth was logistic, and initial average prey density (N_0) was 100. Average predator density (P_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different predator spatial arrangements; some lines may overlap where interaction strengths were similar.

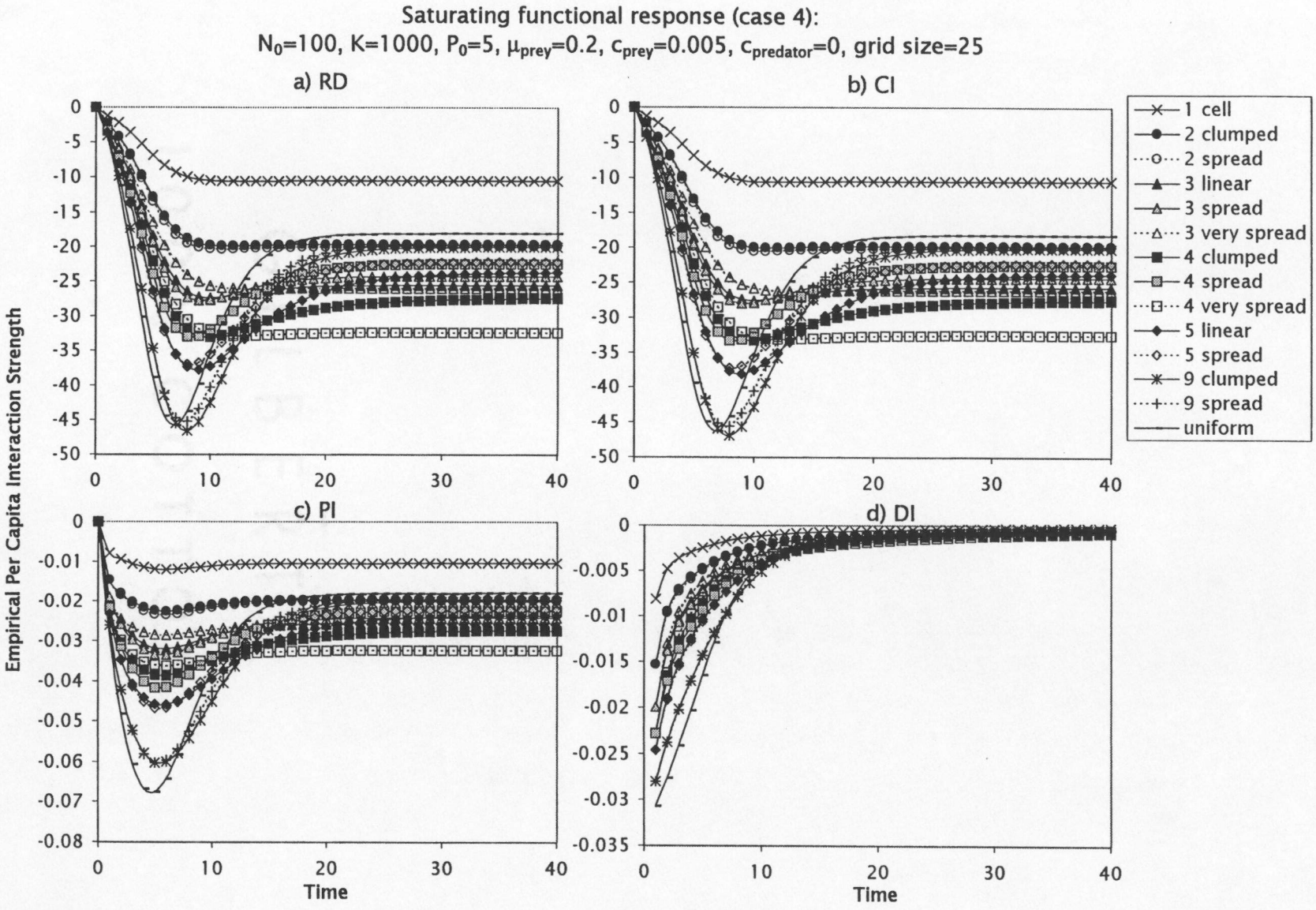

Saturating functional response (case 4):
N_0=100, K=1000, P_0=5, μ_{prey}=0.2, c_{prey}=0.005, $c_{predator}$=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical Per Capita Interaction Strength
Time
1 cell
2 clumped
2 spread
3 linear
3 spread
3 very spread
4 clumped
4 spread
4 very spread
5 linear
5 spread
9 clumped
9 spread
uniform

FIGURE 12. Temporal trajectories of the per capita interaction strength for each of the different predator spatial arrangements (Fig. 2) on a 25 cell grid, as measured by the different indices, estimated from simulations with vs. without predators, for case 4 (Table 1), where predator functional response was a saturating function of prey density (c_{prey}=0.005), prey growth was logistic, and initial average prey density (N_0) was 500. Average predator density (P_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different predator spatial arrangements; some lines may overlap where interaction strengths were similar.

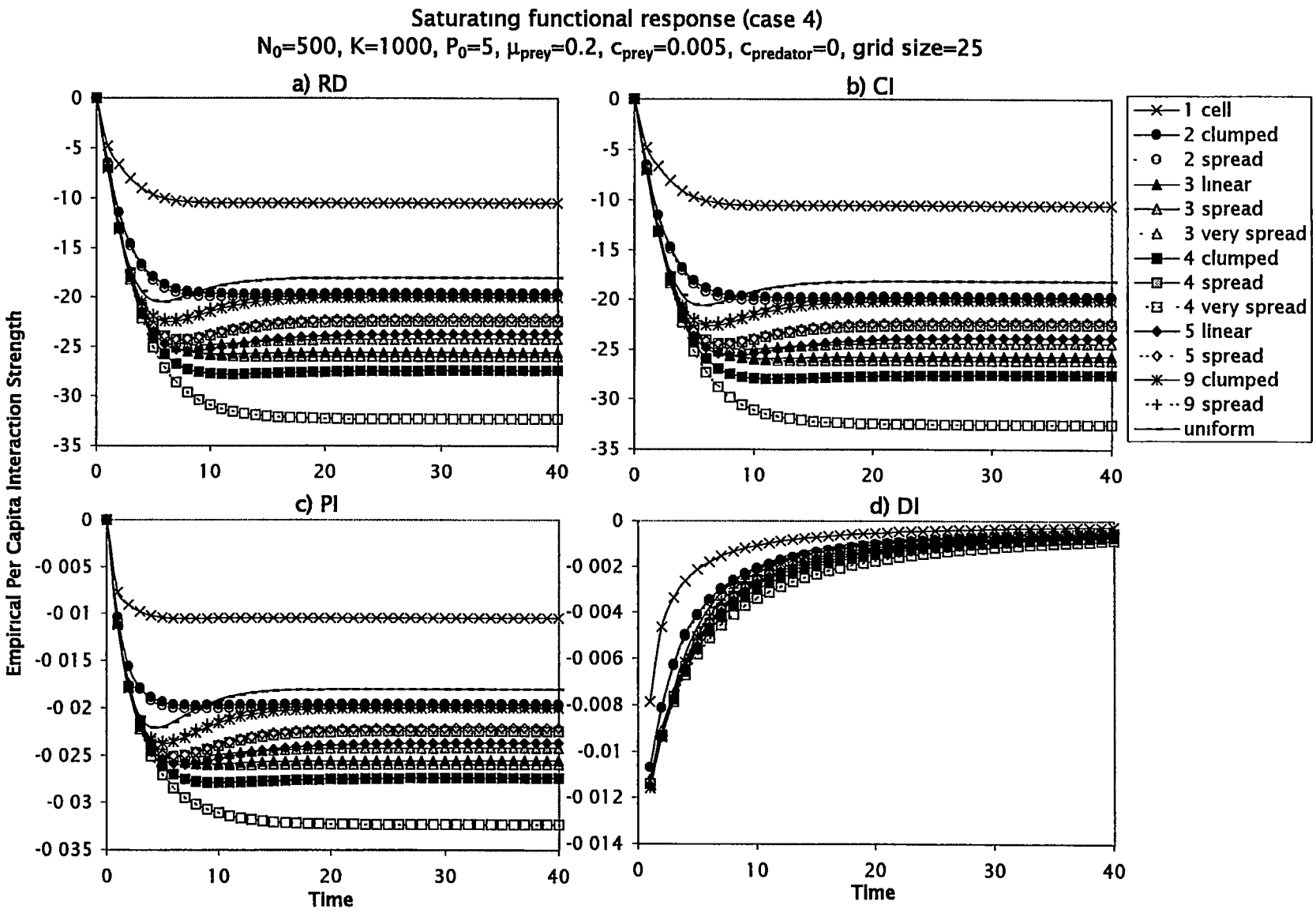

Saturating functional response (case 4)
N0=500, K=1000, P0=5, μprey=0.2, cprey=0.005, cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical Per Capita Interaction Strength
Time
1 cell
2 clumped
2 spread
3 linear
3 spread
3 very spread
4 clumped
4 spread
4 very spread
5 linear
5 spread
9 clumped
9 spread
uniform

FIGURE 13. Temporal trajectories of the per capita interaction strength for each of the different predator spatial arrangements (Fig. 2) on a 25 cell grid, as measured by the different indices, estimated from simulations with vs. without predators, for case 4 (Table 1), where predator functional response was a saturating function of prey density (c_{prey}=0.005), prey growth was logistic, and initial average prey density (N_0) was 1000. Average predator density (P_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. Temporal trajectories for initial average prey densities 1500 and 2000 were qualitatively similar to initial prey density 1000, but varied in the order of interaction strengths from most to least negative, and are not shown. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different predator spatial arrangements; some lines may overlap where interaction strengths were similar.

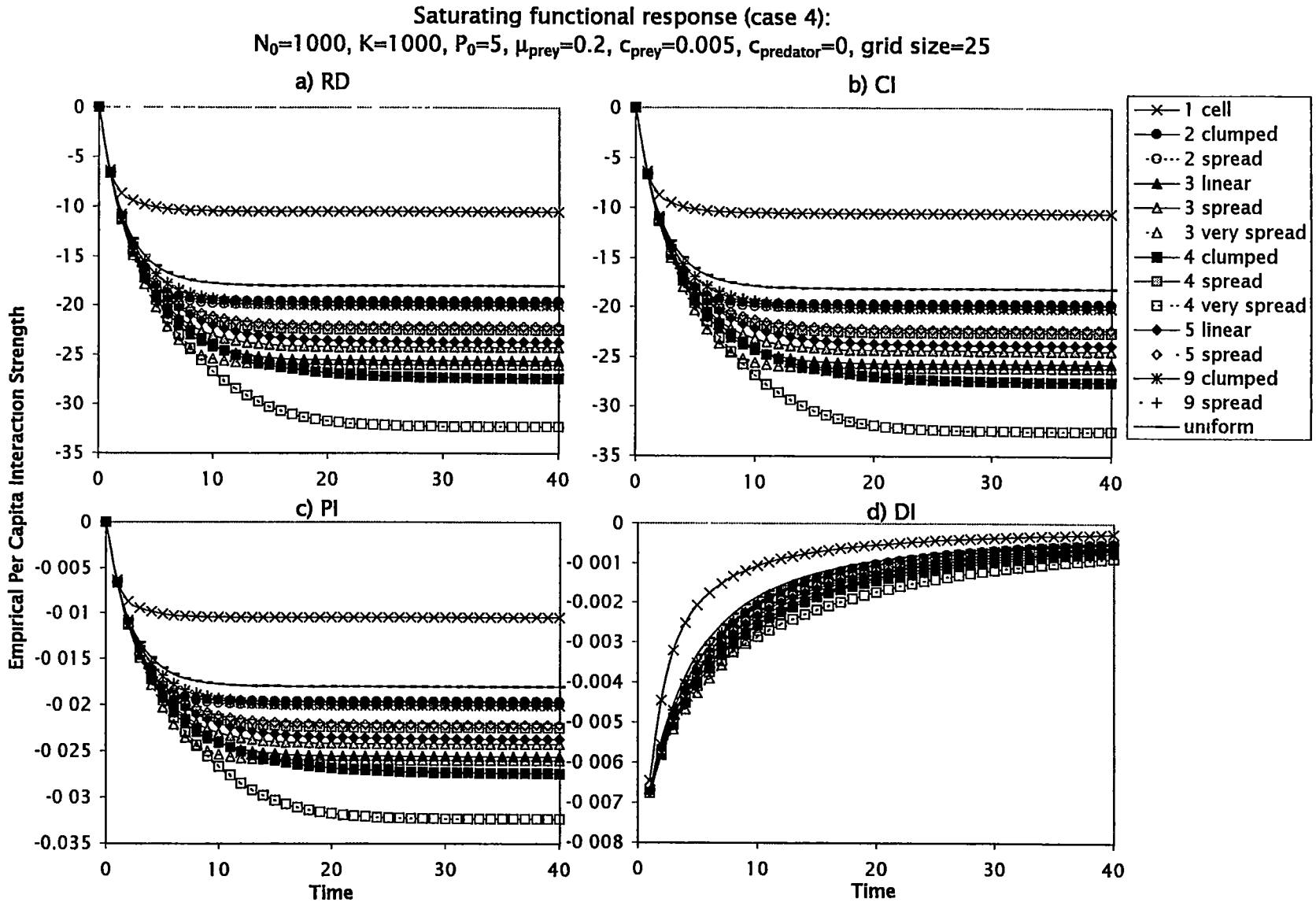

Saturating functional response (case 4):
N0=1000, K=1000, P0=5, μprey=0.2, cprey=0.005, cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical Per Capita Interaction Strength
Time
1 cell
2 clumped
2 spread
3 linear
3 spread
3 very spread
4 clumped
4 spread
4 very spread
5 linear
5 spread
9 clumped
9 spread
uniform

FIGURE 14. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 25 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 4 (Table 1), where prey growth was logistic, predator functional response was a saturating function of prey density (c_{prey}=0.005), initial average prey density (N_0) ranged from 100 to 2000, and average predator density (P_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

Saturating functional response, constant carrying capacity (case 4):
K=1000, P_0=5, μ_{prey}=0.2, c_{prey}=0.005, $c_{predator}$=0, grid size=25

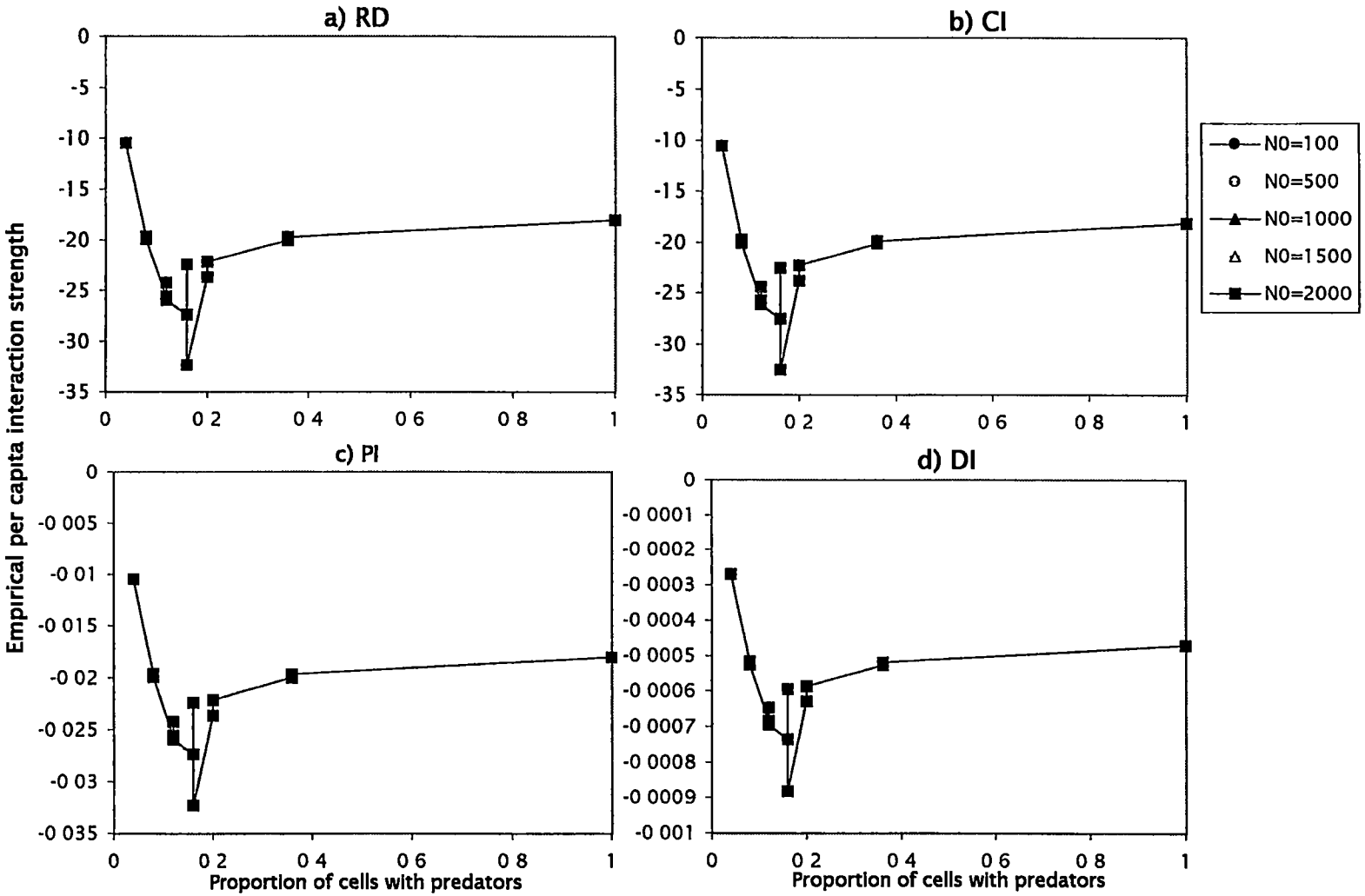


FIGURE 15. Temporal trajectories of the per capita interaction strength for each of the different predator spatial arrangements (Fig. 2) on a 25 cell grid, as measured by the different indices, estimated from simulations with vs. without predators, for case 5 (Table 1), where predator functional response was linear ($c_{prey}=c_{predator}=0$), prey growth was logistic, and initial average prey density was equal to carrying capacity ($N_0=K=100$). Average predator density (P_0) and prey dispersal ability (μ_{prey}) were held constant across all runs. Temporal trajectories for $N_0=K=500$, $N_0=K=1000$, $N_0=K=1500$, $N_0=K=2000$ were qualitatively similar to $N_0=K=100$, and are not shown. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different predator spatial arrangements; some lines may overlap where interaction strengths were similar.

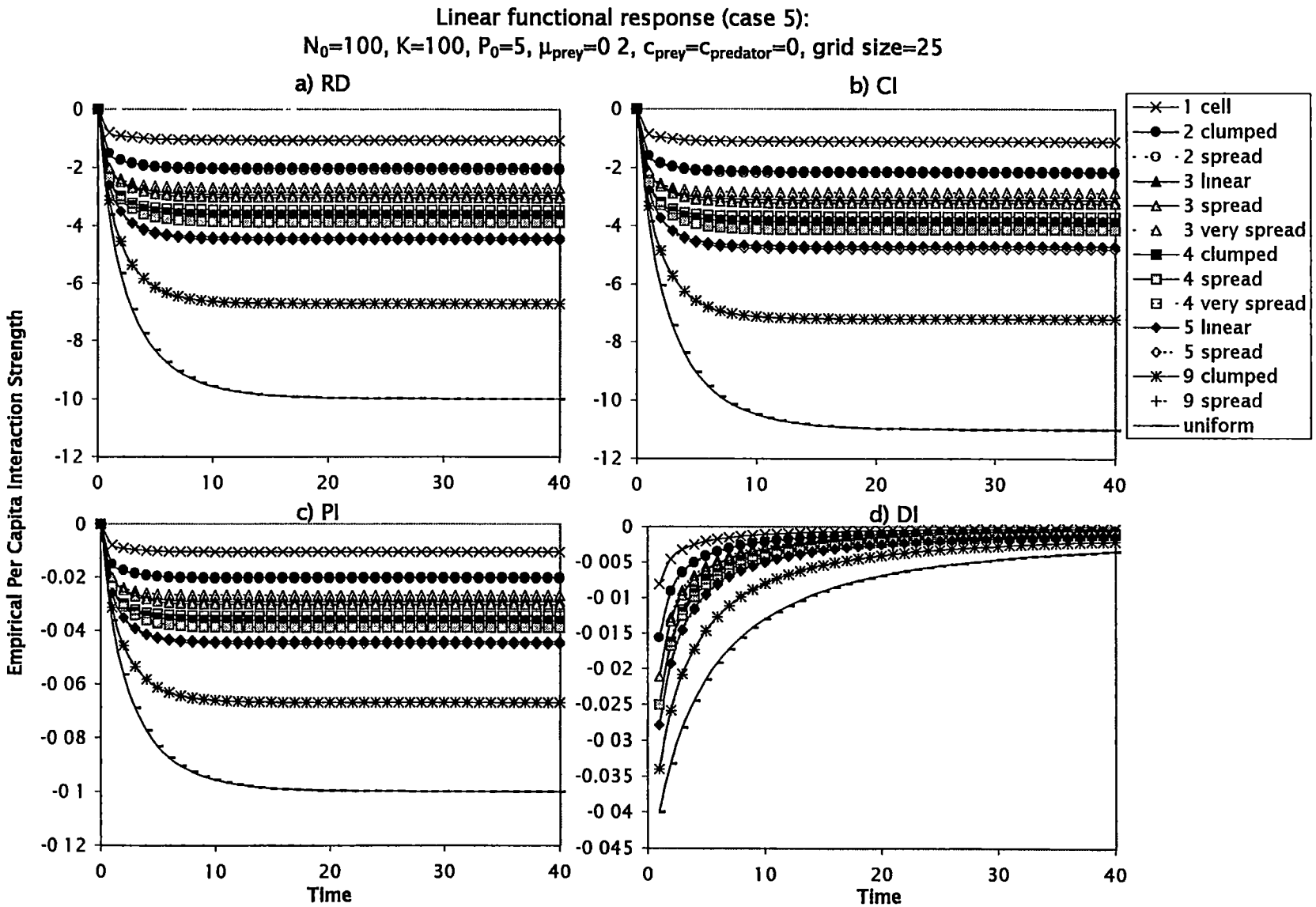

Linear functional response (case 5):
N0=100, K=100, P0=5, μprey=0 2, cprey=cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical Per Capita Interaction Strength
Time
1 cell
2 clumped
2 spread
3 linear
3 spread
3 very spread
4 clumped
4 spread
4 very spread
5 linear
5 spread
9 clumped
9 spread
uniform

FIGURE 16. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 25 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 5 (Table 1), where prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$), and initial average prey density was equal to carrying capacity ($N_0=K$) and ranged from 100 to 2000. Average predator density (P_0) and prey dispersal ability (μ_{prey}) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

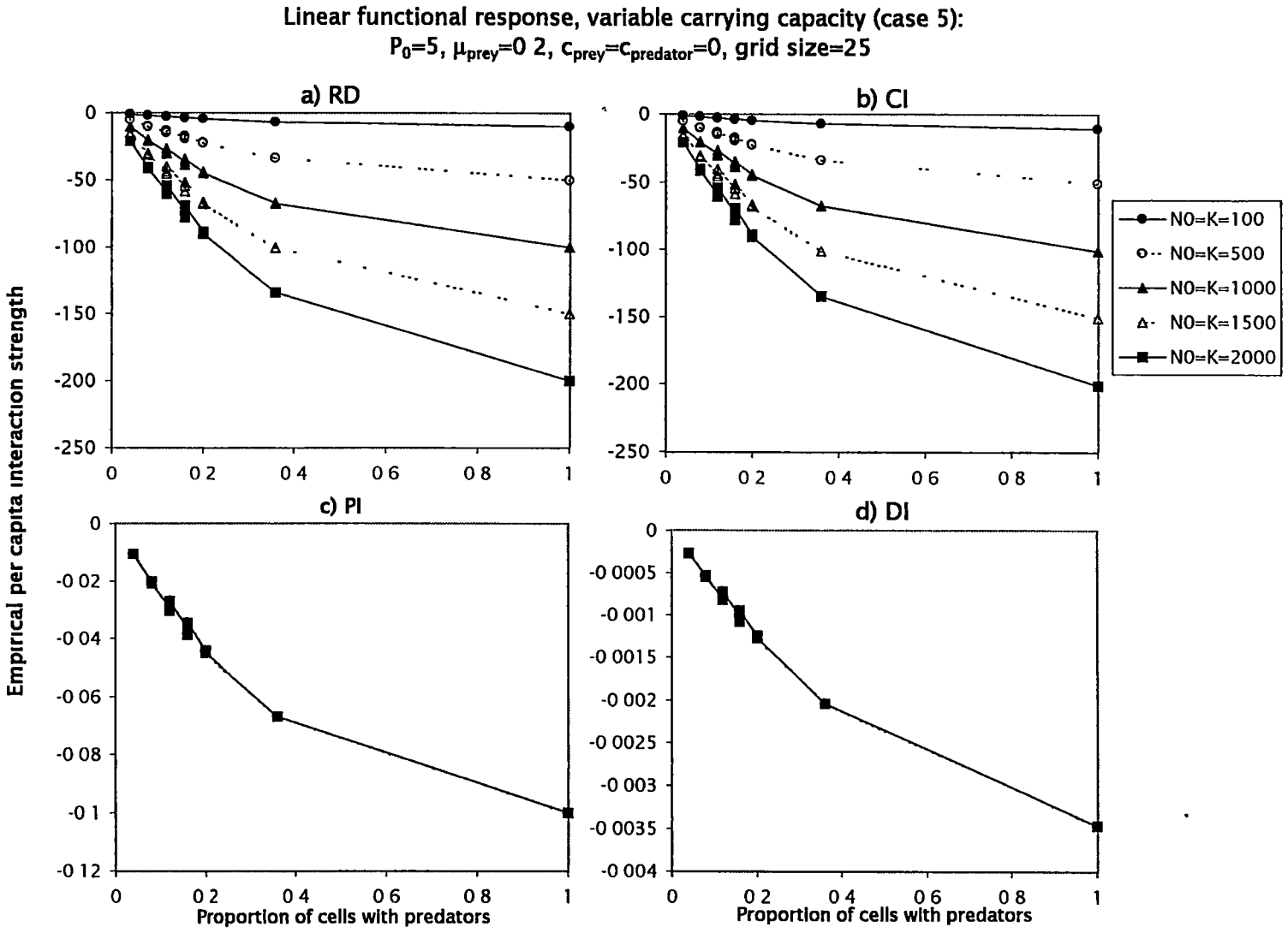

Linear functional response, variable carrying capacity (case 5):
P_0=5, μ_{prey}=0 2, c_{prey}=$c_{predator}$=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Proportion of cells with predators
Proportion of cells with predators
N0=K=100
N0=K=500
N0=K=1000
N0=K=1500
N0=K=2000

FIGURE 17. Temporal trajectories of the per capita interaction strength for each of the different predator spatial arrangements (Fig. 2) on a 25 cell grid, as measured by the different indices, estimated from simulations with vs. without predators, for case 6 (Table 1), where predator functional response was a saturating function of prey density (c_{prey}=0.005), prey growth was logistic, and initial average prey density was equal to carrying capacity, N_0=K=500. Average predator density (P_0) and prey dispersal ability (μ_{prey}) were held constant across all runs. Temporal trajectories for N_0=K=100, N_0=K=1000 (Fig. 12), N_0=K=1500, N_0=K=2000 were qualitatively similar to N_0=K=500, but varied in the order of interaction strengths from most to least negative, and are not shown. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different predator spatial arrangements; some lines may overlap where interaction strengths were similar.

Saturating functional response (case 6):
N_0=500, K=500, P_0=5, μ_{prey}=0.2, c_{prey}=0.005, $c_{predator}$=0, grid size=25

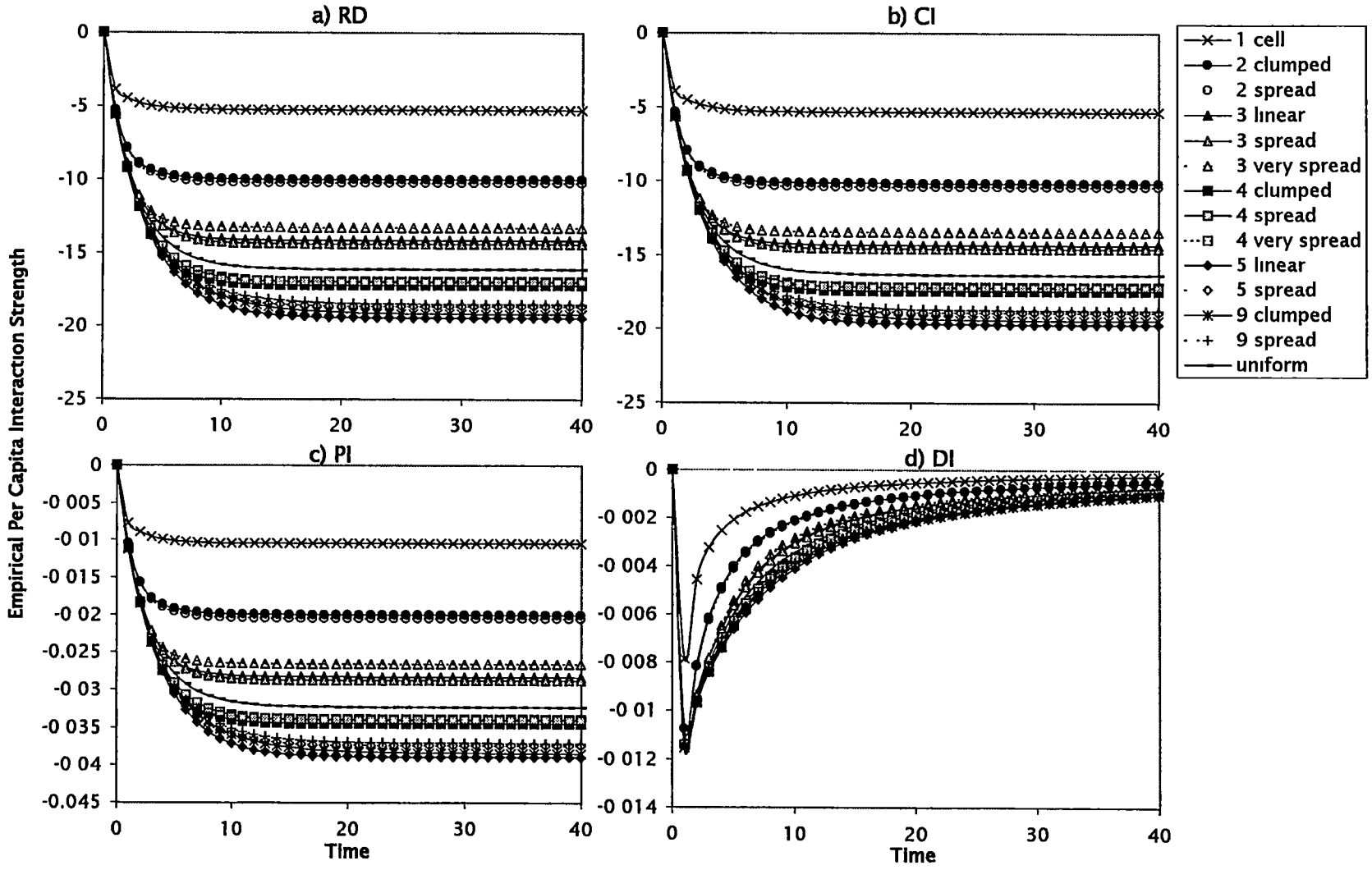


FIGURE 18. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 25 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 6 (Table 1), where prey growth was logistic, predator functional response was a saturating function of prey density (c_{prey}=0.005), and initial average prey density was equal to carrying capacity (N_0=K) and ranged from 100 to 2000. Average predator density (P_0) and prey dispersal ability (μ_{prey}) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

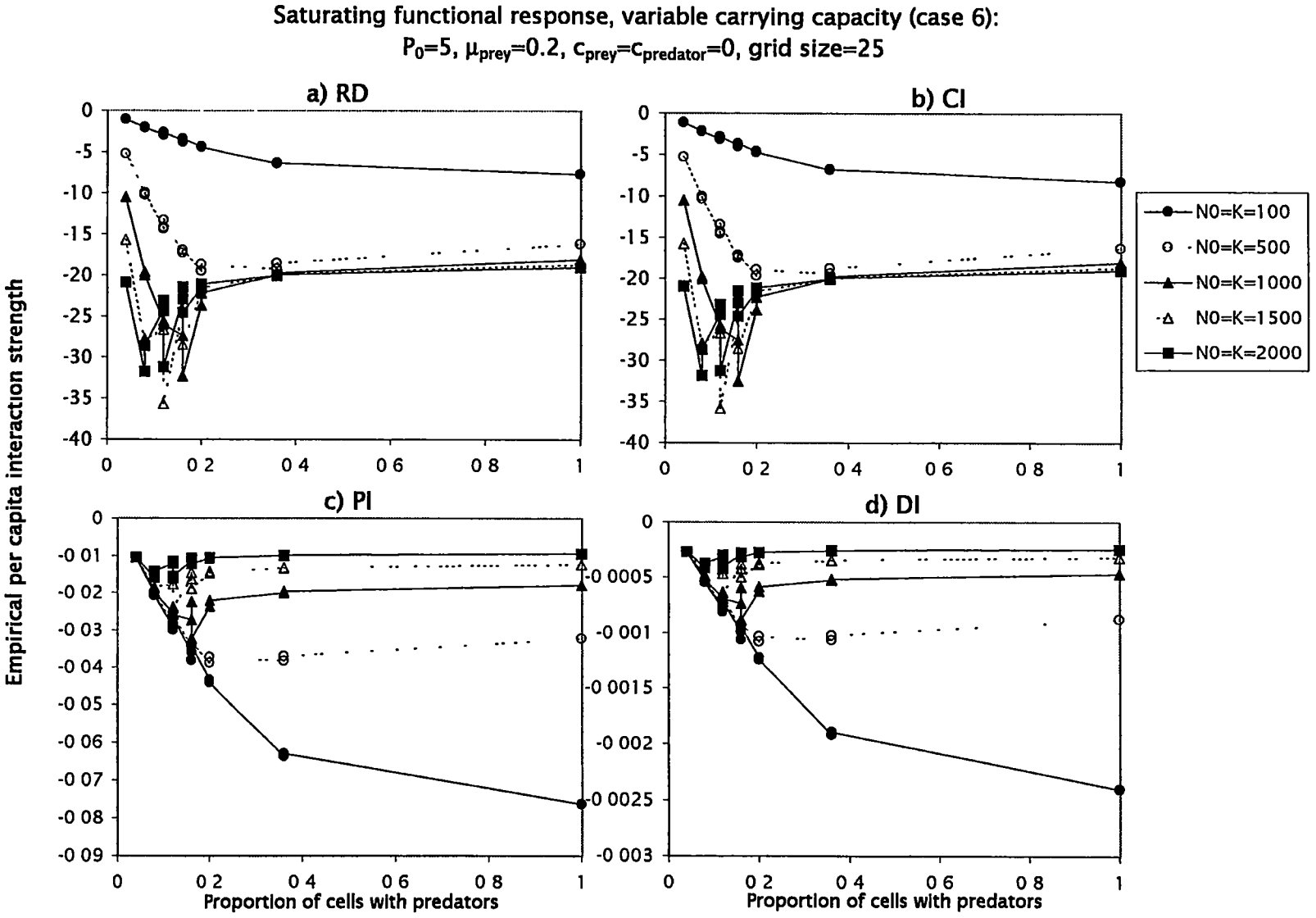

Saturating functional response, variable carrying capacity (case 6):
P0=5, μprey=0.2, cprey=cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Proportion of cells with predators
Proportion of cells with predators
N0=K=100
N0=K=500
N0=K=1000
N0=K=1500
N0=K=2000

FIGURE 19. Relation of proportion of cells with predators for logistic prey growth and saturating functional response (Table 1, case 6) to the coefficient of variation (CV) for each of the four interaction strengths (RD, CI, PI, and DI) for a particular proportion of cells with predators. Each point gives the CV over all interaction strengths, with N_0=K ranging from 100 to 2000 and predator distributions ranging from clumped to spread, for a particular proportion of cells with predators.

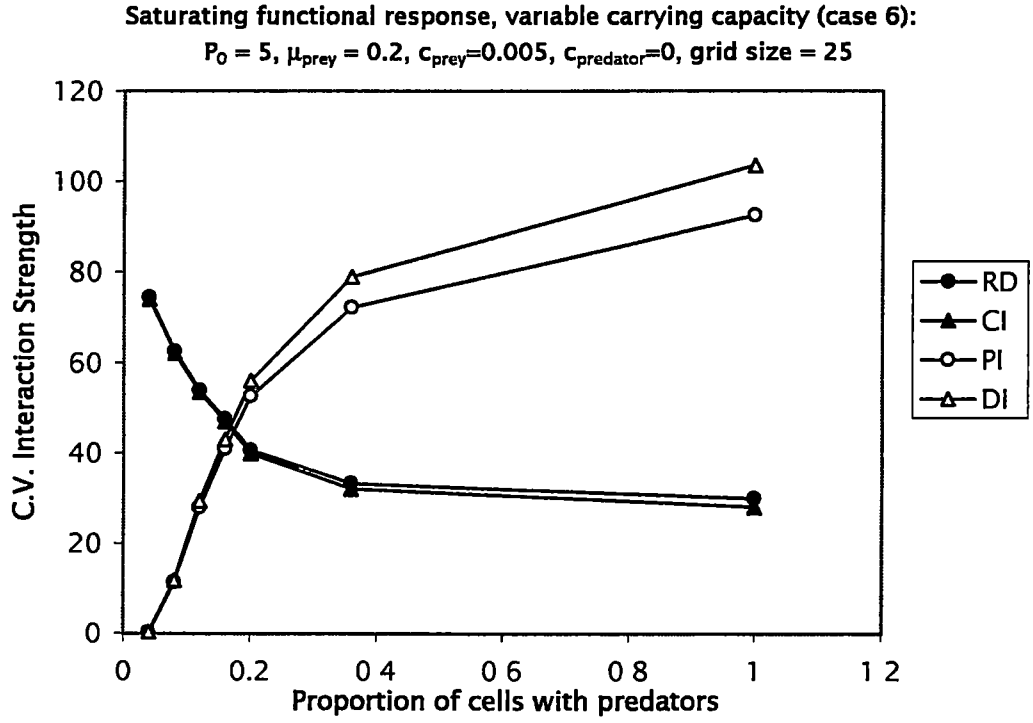


FIGURE 20. Relation of prey carrying capacity (K) with logistic prey growth and saturating functional response (Table 1; case 6) to the coefficient of variation (CV) for the raw difference (RD) among different predator spatial distributions (linear, clumped, spread, and very spread) for a particular number of cells with predators. Each of the five symbols gives the CV among the following predator distributions (see Fig. 2): i) 2 clumped, spread; ii) 3 linear, spread, very spread; iii) 4 clumped, spread, very spread; iv) 5 linear, spread; and v) 9 clumped, spread. Patterns for the coefficient of variation in CI, PI, and DI were qualitatively similar to that of RD.

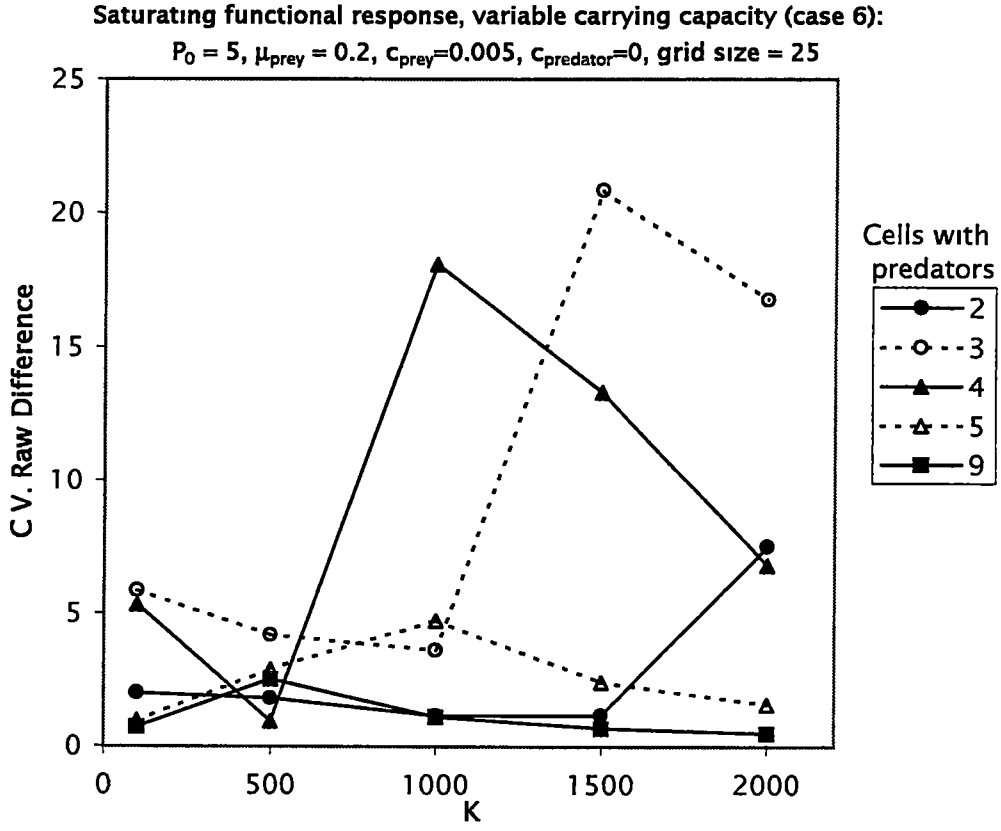


FIGURE 21. Temporal trajectories of the per capita interaction strength for each of the different predator spatial arrangements (Fig. 2) on a 25 cell grid, as measured by the different indices, estimated from simulations with vs. without predators, for case 8 (Table 1), where prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$), and average predator density (P_0) was 1. Average initial prey density (N_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. Temporal trajectories for average predator density 5 were qualitatively similar to average predator density 1, and are not shown. Temporal trajectories with predator interference (case 10; $c_{predator}=0.1$) for average predator densities ranging from 1 to 20 were also qualitatively similar, and are not shown. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different predator spatial arrangements; some lines may overlap where interaction strengths were similar.

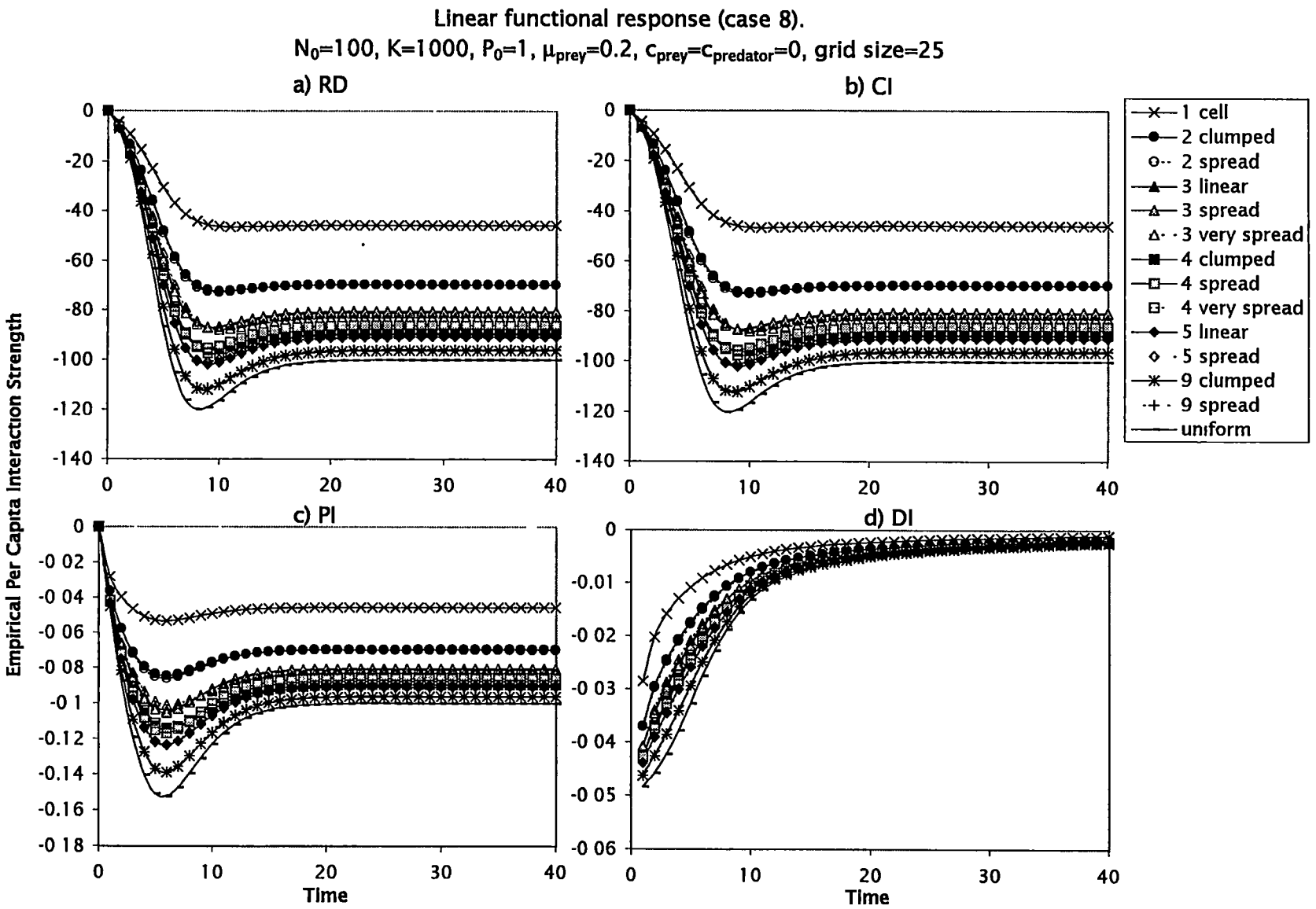

Linear functional response (case 8).
N0=100, K=1000, P0=1, μprey=0.2, cprey=cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical Per Capita Interaction Strength
Time
1 cell
2 clumped
2 spread
3 linear
3 spread
3 very spread
4 clumped
4 spread
4 very spread
5 linear
5 spread
9 clumped
9 spread
uniform

FIGURE 22. Temporal trajectories of the per capita interaction strength for each of the different predator spatial arrangements (Fig. 2) on a 25 cell grid, as measured by the different indices, estimated from simulations with vs. without predators, for case 8 (Table 1), where prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$), and average predator density (P_0) was 20. Average initial prey density (N_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. Temporal trajectories for average predator density 10 and 15 were qualitatively similar to average predator density 20, and are not shown. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different predator spatial arrangements; some lines may overlap where interaction strengths were similar.

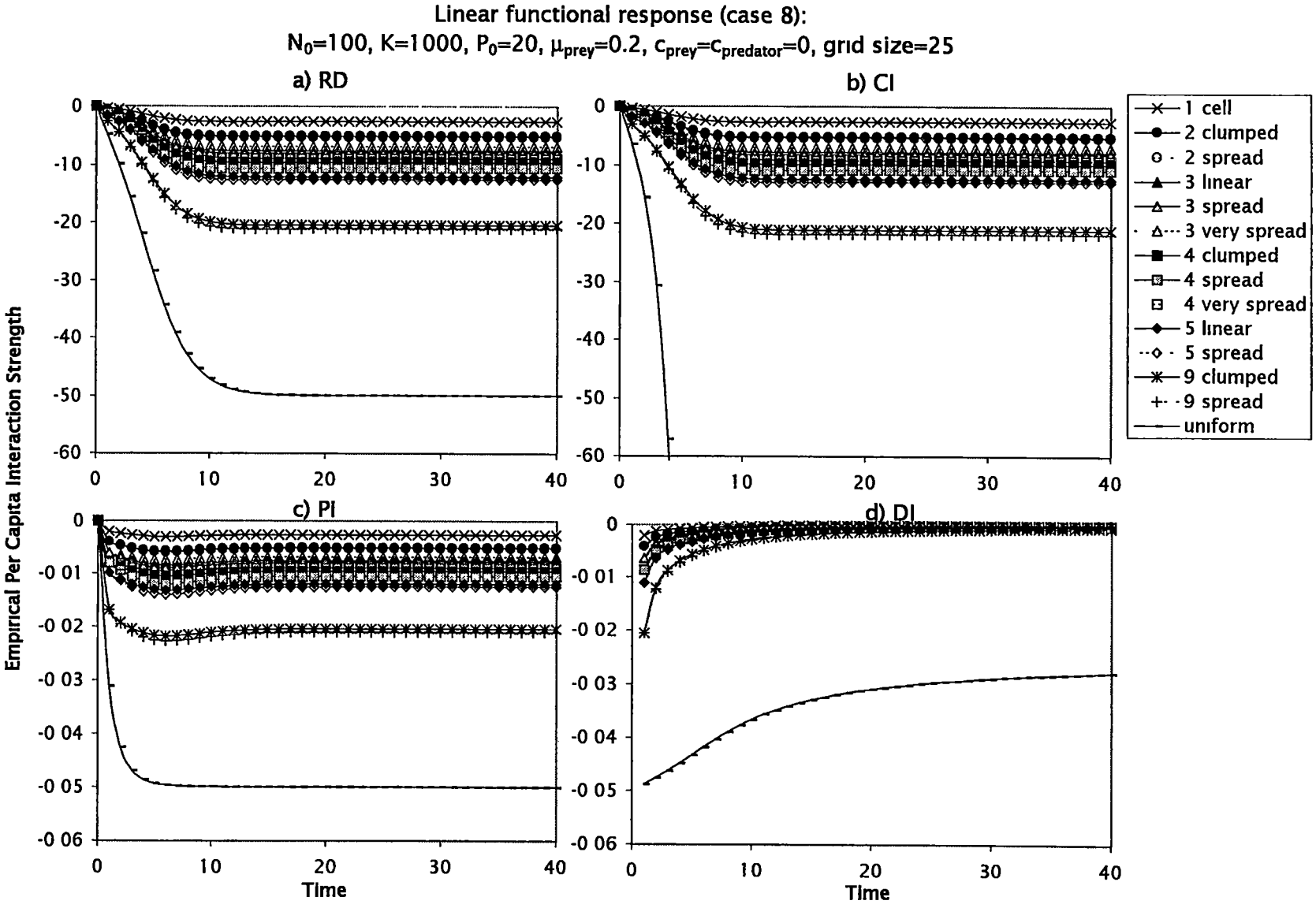

Linear functional response (case 8):
N0=100, K=1000, P0=20, μprey=0.2, cprey=cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical Per Capita Interaction Strength
Time
Time
1 cell
2 clumped
2 spread
3 linear
3 spread
3 very spread
4 clumped
4 spread
4 very spread
5 linear
5 spread
9 clumped
9 spread
uniform

FIGURE 23. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 25 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 8 (Table 1), where prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$), average predator density (P_0) ranged from 1 to 20, and initial average prey density (N_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

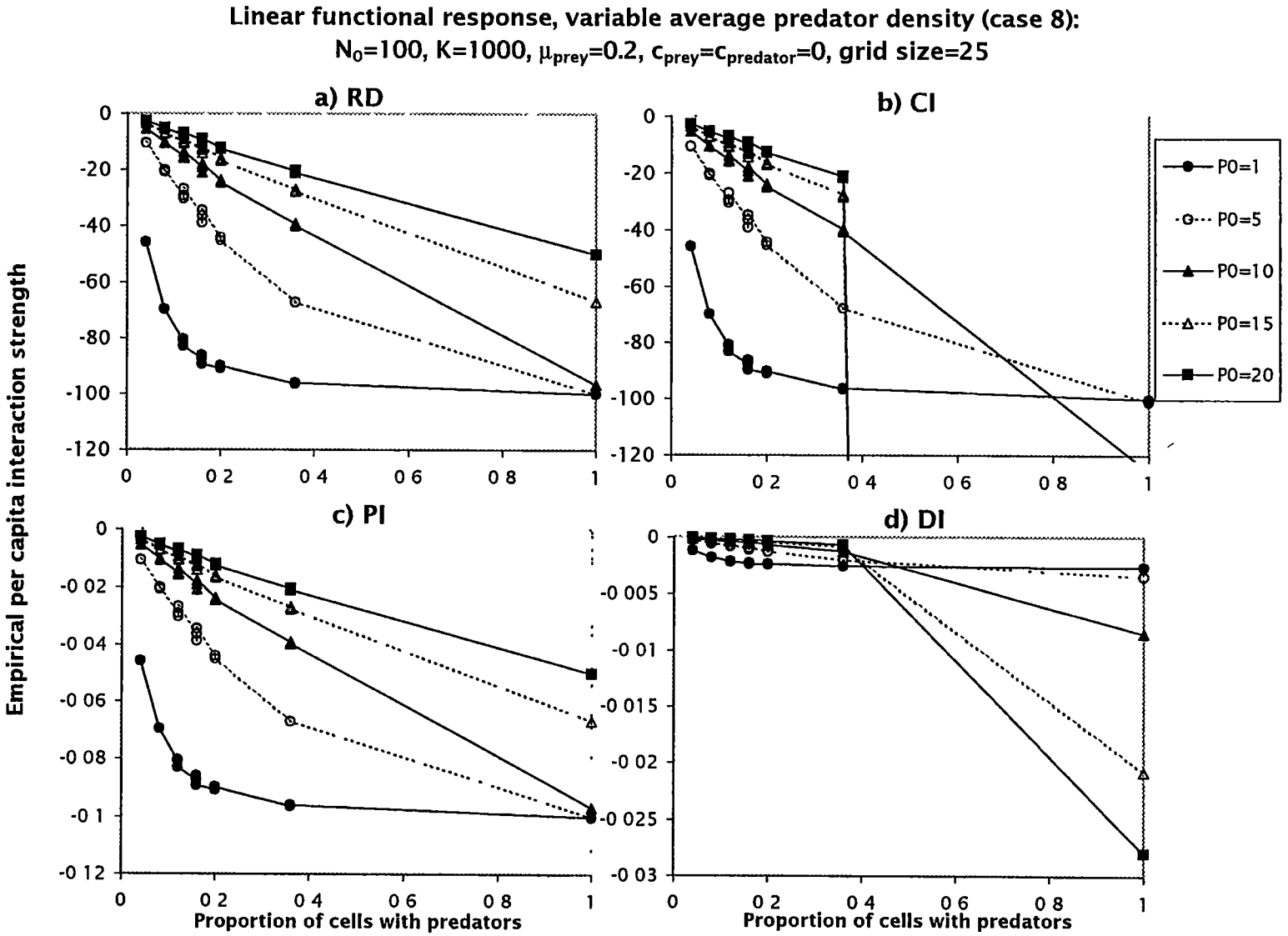

Linear functional response, variable average predator density (case 8):
N0=100, K=1000, μprey=0.2, cprey=cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Proportion of cells with predators
Proportion of cells with predators
P0=1
P0=5
P0=10
P0=15
P0=20

FIGURE 24. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 25 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 10 (Table 1), where prey growth was logistic, predator functional response incorporated predator interference ($c_{predator}$=0.1), average predator density (P_0) ranged from 1 to 20, and initial average prey density (N_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

Predator interference, variable average predator density (case 10):
N_0=100, K=1000, μ_{prey}=0.2, c_{prey}=0, $c_{predator}$=0.1, grid size=25

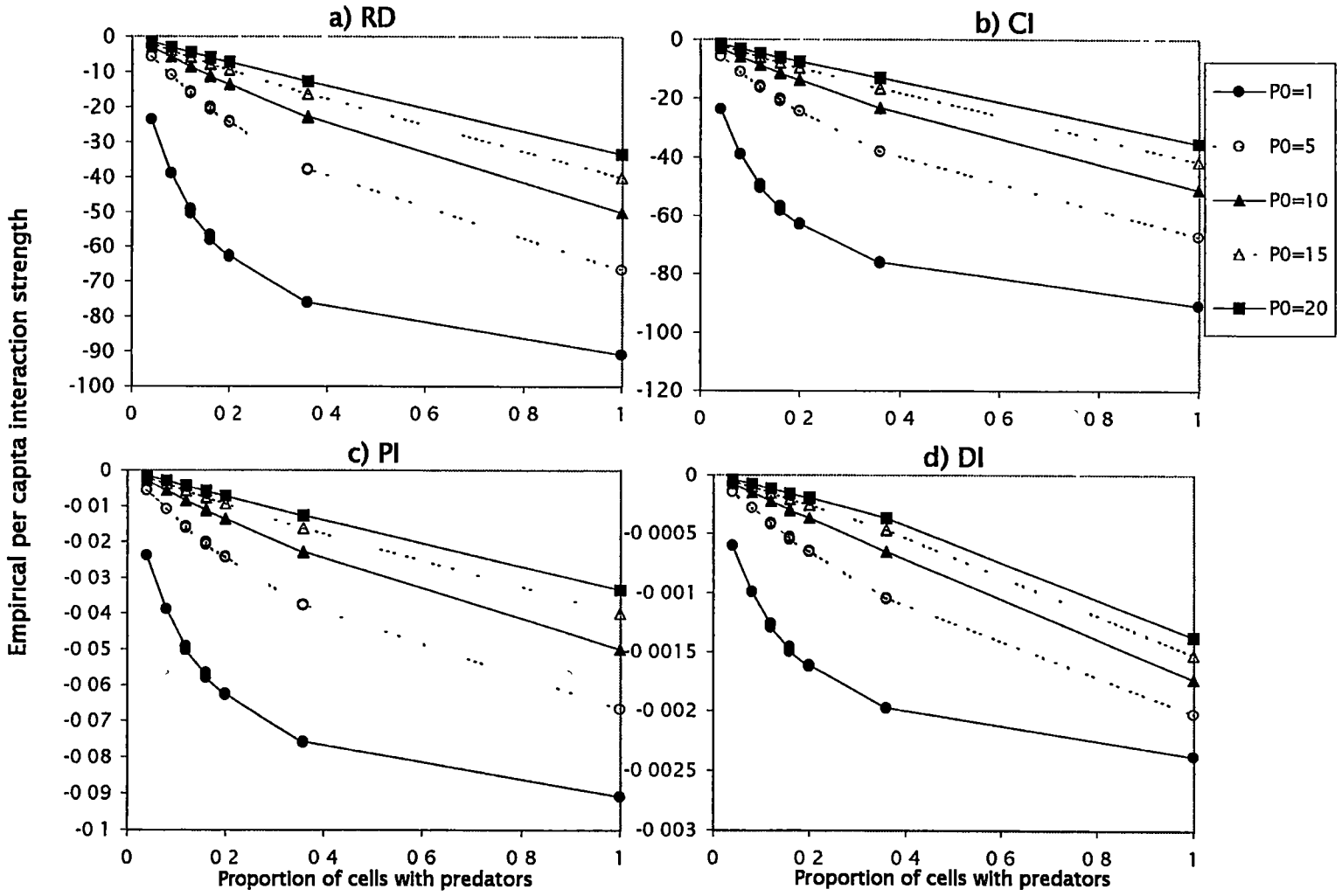


FIGURE 25. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 9 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 7 (Table 1), where prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$), average predator density (P_0) ranged from 1 to 20, and initial average prey density (N_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

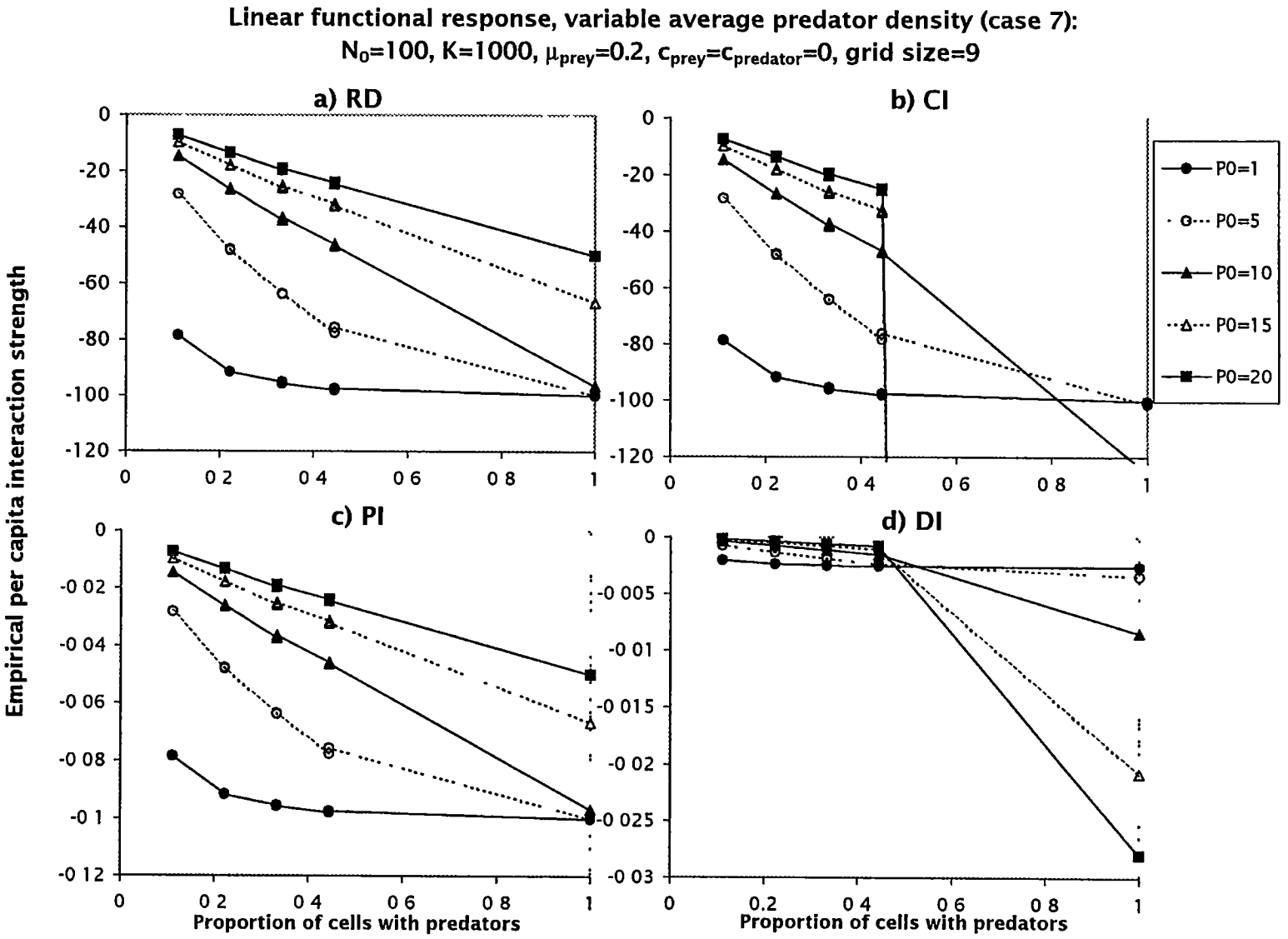

Linear functional response, variable average predator density (case 7):
N0=100, K=1000, μprey=0.2, cprey=cpredator=0, grid size=9
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Proportion of cells with predators
Proportion of cells with predators
P0=1
P0=5
P0=10
P0=15
P0=20

FIGURE 26. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 49 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 9 (Table 1), where prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$), average predator density (P_0) ranged from 1 to 20, and initial average prey density (N_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

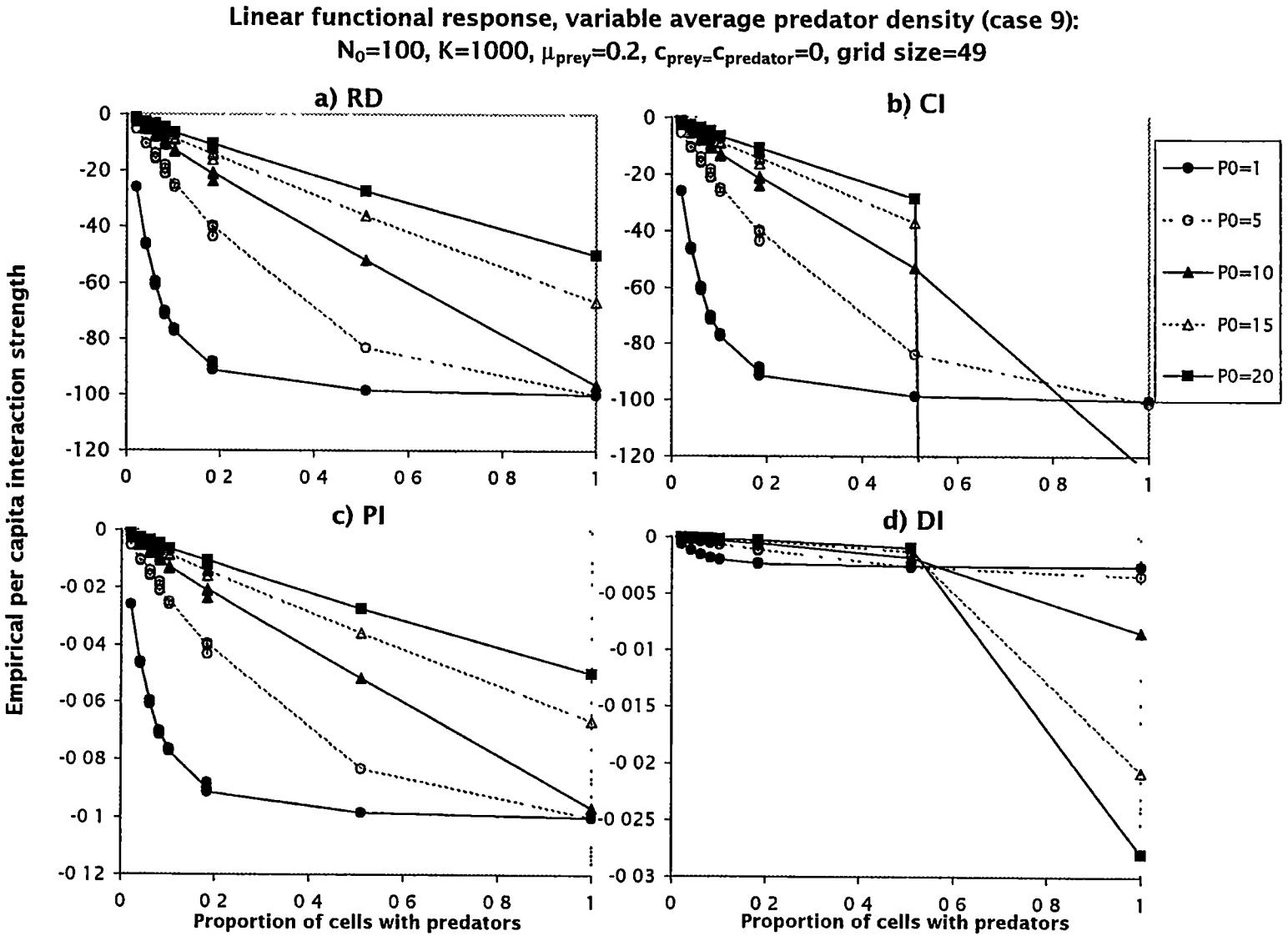

Linear functional response, variable average predator density (case 9):
N0=100, K=1000, μprey=0.2, cprey=cpredator=0, grid size=49
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Proportion of cells with predators
Proportion of cells with predators
P0=1
P0=5
P0=10
P0=15
P0=20

FIGURE 27. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 49 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 11 (Table 1), where prey growth was logistic, predator functional response incorporated predator interference ($c_{predator}$=0.1), average predator density (P_0) ranged from 1 to 20, and initial average prey density (N_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions. clumped, linear, spread, or very spread (Fig. 2).

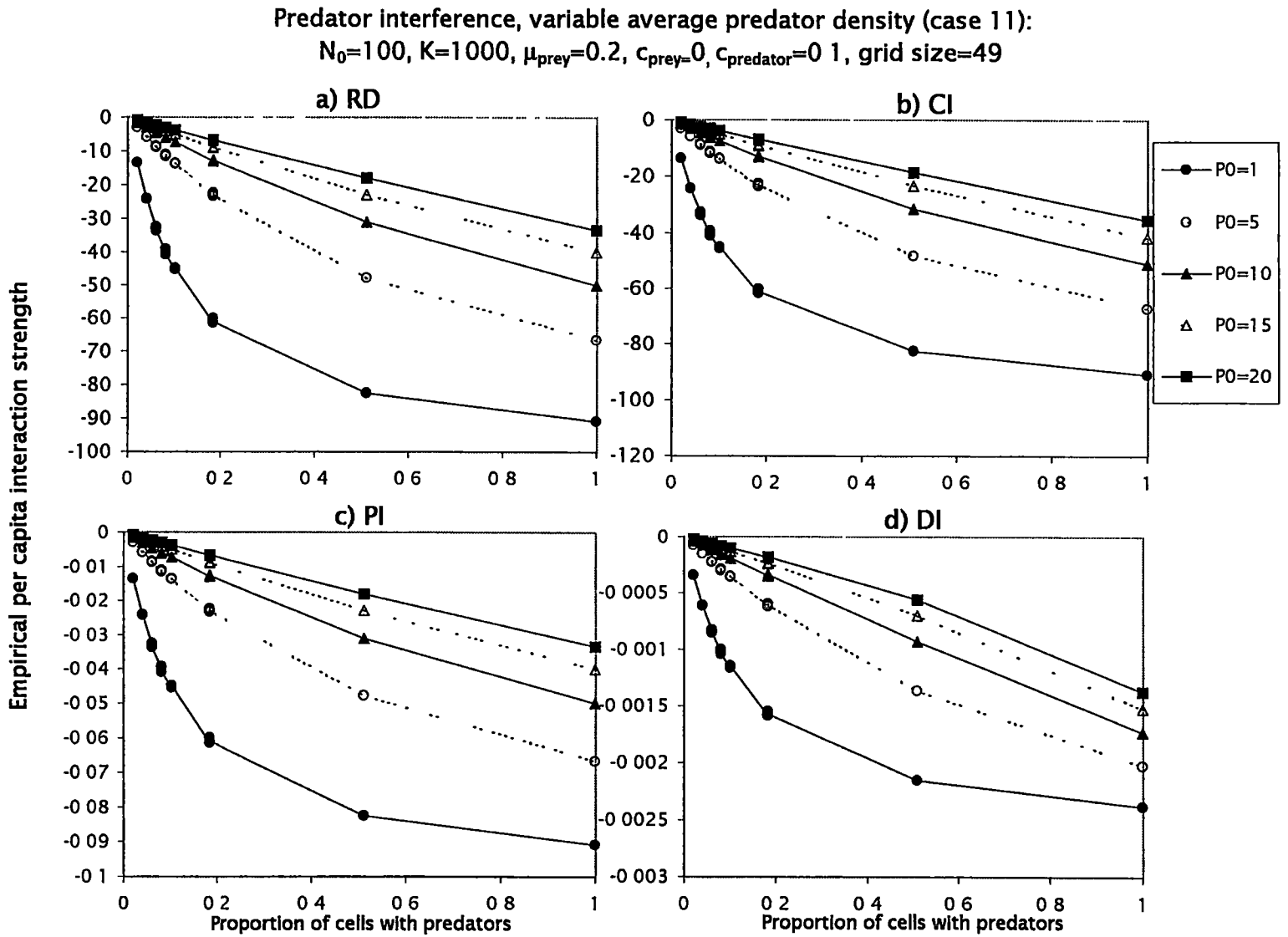

Predator interference, variable average predator density (case 11):
N0=100, K=1000, μprey=0.2, cprey=0, cpredator=0 1, grid size=49
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Proportion of cells with predators
Proportion of cells with predators
P0=1
P0=5
P0=10
P0=15
P0=20

FIGURE 28. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) quantified by local predator density in a single predator-occupied cell (total predator number in spatial grid/number of cells occupied by predators), as measured by the different indices, estimated from simulations with vs. without predators, for cases 7, 8, and 9 (Table 1), where prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$). Average predator density (P_0) ranged from 1 to 20 and grid spatial extents were 9, 25, or 49 cells. Initial average prey density (N_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different initial average prey densities for different spatial extents; where only one line is visible, all fifteen lines overlap.

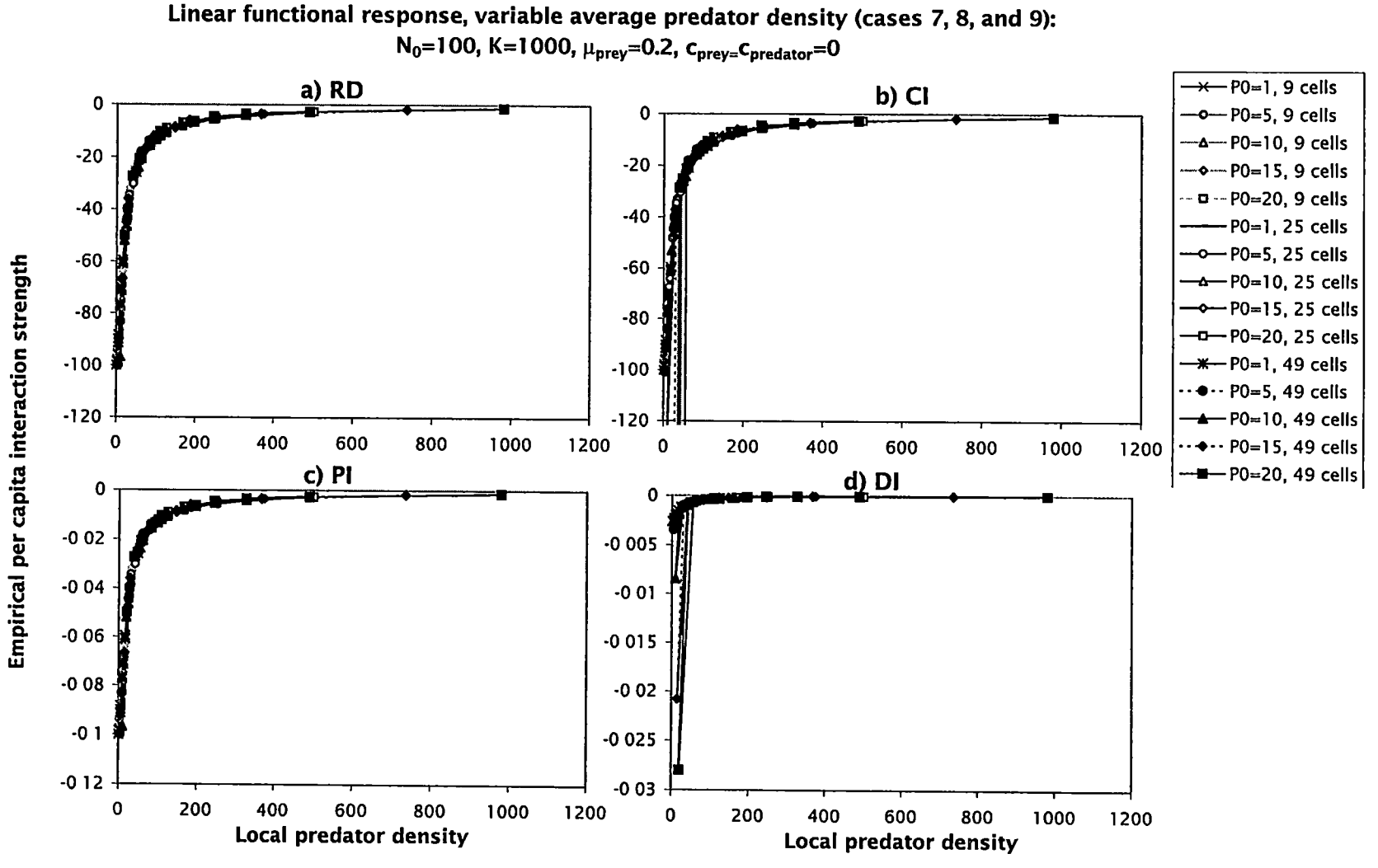

Linear functional response, variable average predator density (cases 7, 8, and 9):
N0=100, K=1000, μprey=0.2, cprey=cpredator=0
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Local predator density
Local predator density
P0=1, 9 cells
P0=5, 9 cells
P0=10, 9 cells
P0=15, 9 cells
P0=20, 9 cells
P0=1, 25 cells
P0=5, 25 cells
P0=10, 25 cells
P0=15, 25 cells
P0=20, 25 cells
P0=1, 49 cells
P0=5, 49 cells
P0=10, 49 cells
P0=15, 49 cells
P0=20, 49 cells

FIGURE 29. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) quantified by local predator density in a single predator-occupied cell (total predator number in spatial grid/number of cells occupied by predators), as measured by the different indices, estimated from simulations with vs. without predators, for cases 10 and 11 (Table 1), where prey growth was logistic, predator interference was incorporated ($c_{predator}$=0.1). Average predator density (P_0) ranged from 1 to 20 and grid spatial extents were 25 or 49 cells. Initial average prey density (N_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities for different spatial extents; where only one line is visible, all ten lines overlap.

Predator interference, variable average predator density (cases 10 and 11):
N_0=100, K=1000, μ_{prey}=0.2, c_{prey}=0, $c_{predator}$=0.1

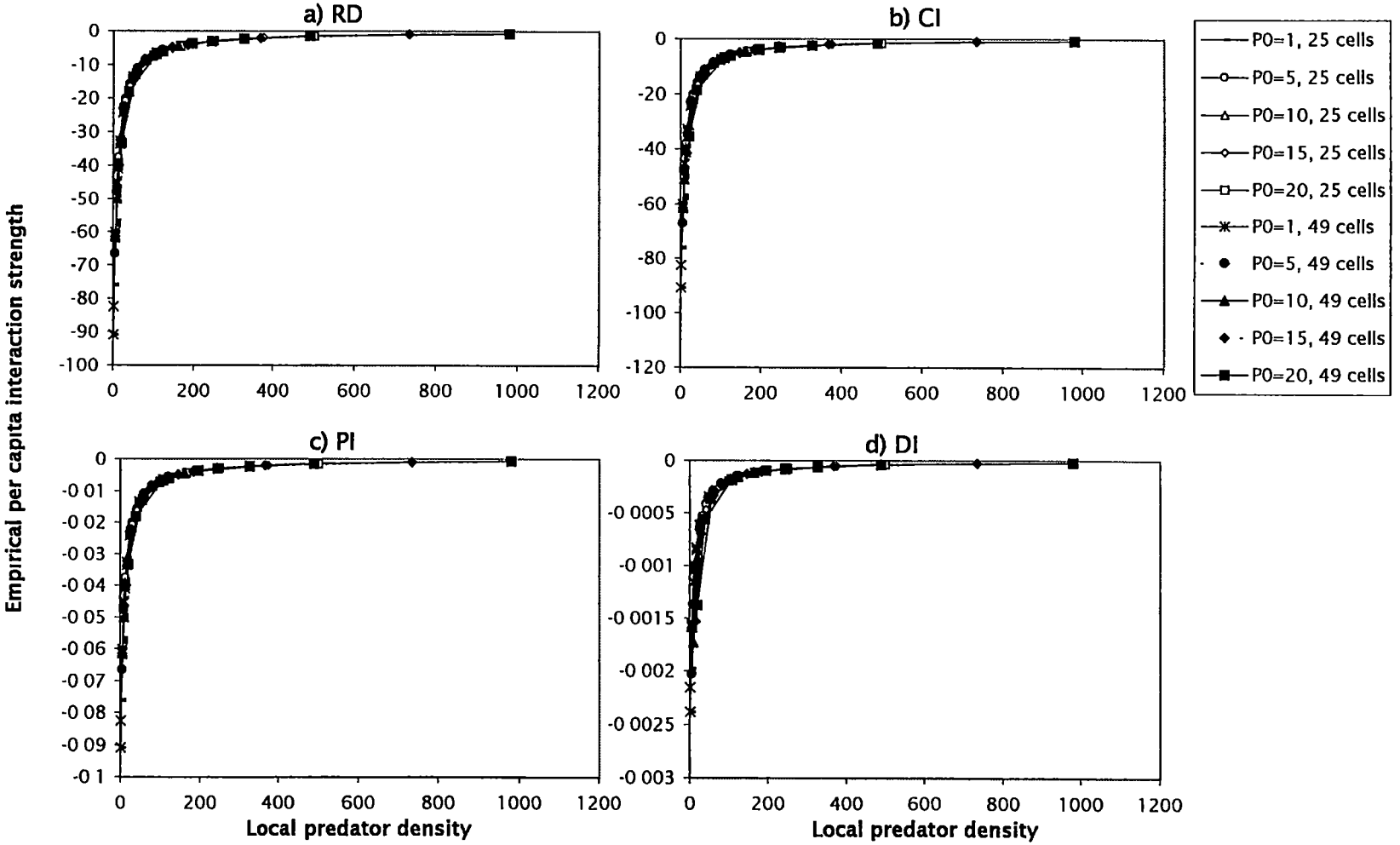


FIGURE 30 Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 25 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 12 (Table 1), where prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$), prey dispersal ability ranged (μ_{prey}) from 0 to 0.8, and initial average prey density (N_0), prey carrying capacity (K), and average predator density (P_0) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

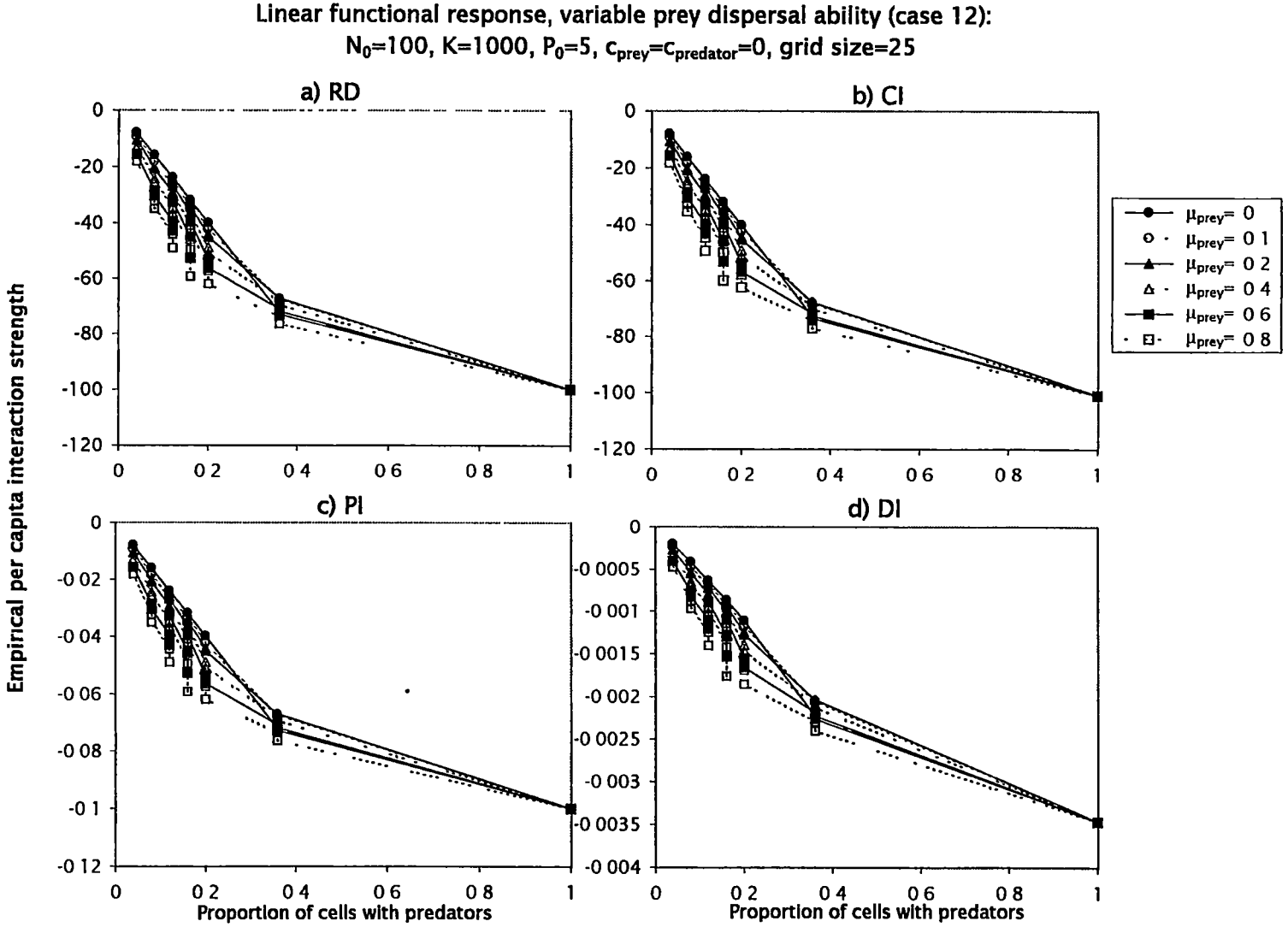

Linear functional response, variable prey dispersal ability (case 12):
N0=100, K=1000, P0=5, cprey=cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Proportion of cells with predators
Proportion of cells with predators
μprey= 0
μprey= 0 1
μprey= 0 2
μprey= 0 4
μprey= 0 6
μprey= 0 8

FIGURE 31. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 49 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 12 (Table 1), where prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$), prey dispersal ability ranged (μ_{prey}) from 0 to 0.8, and initial average prey density (N_0), prey carrying capacity (K), and average predator density (P_0) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different initial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

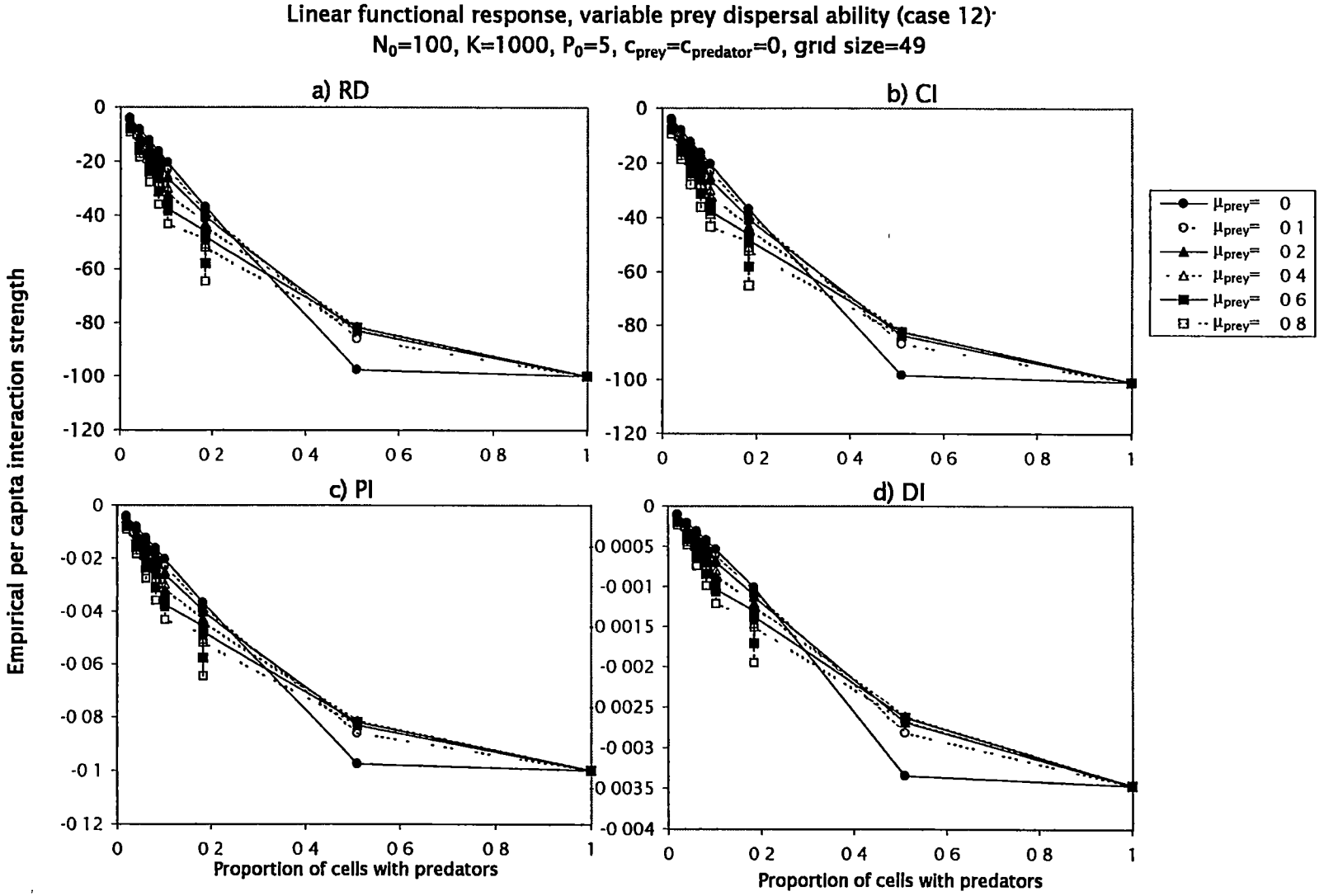

Linear functional response, variable prey dispersal ability (case 12)
N0=100, K=1000, P0=5, cprey=cpredator=0, grid size=49
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Proportion of cells with predators
Proportion of cells with predators
μprey= 0
μprey= 0 1
μprey= 0 2
μprey= 0 4
μprey= 0 6
μprey= 0 8

FIGURE 32. Relation of prey dispersal ability (μ_{prey}) with logistic prey growth and linear functional response (Table 1, case 12) to the coefficient of variation (CV) for the raw difference (RD) among different predator spatial distributions (linear, clumped, spread, and very spread) for a particular number of cells with predators on a 25 cell grid. Each of the five symbols gives the CV among the following predator distributions (see Fig. 2) i) 2 clumped, spread; ii) 3 linear, spread, very spread; iii) 4 clumped, spread, very spread, iv) 5 linear, spread; and v) 9 clumped, spread. Patterns for the coefficient of variation in CI, PI, and DI were qualitatively similar to that of RD.

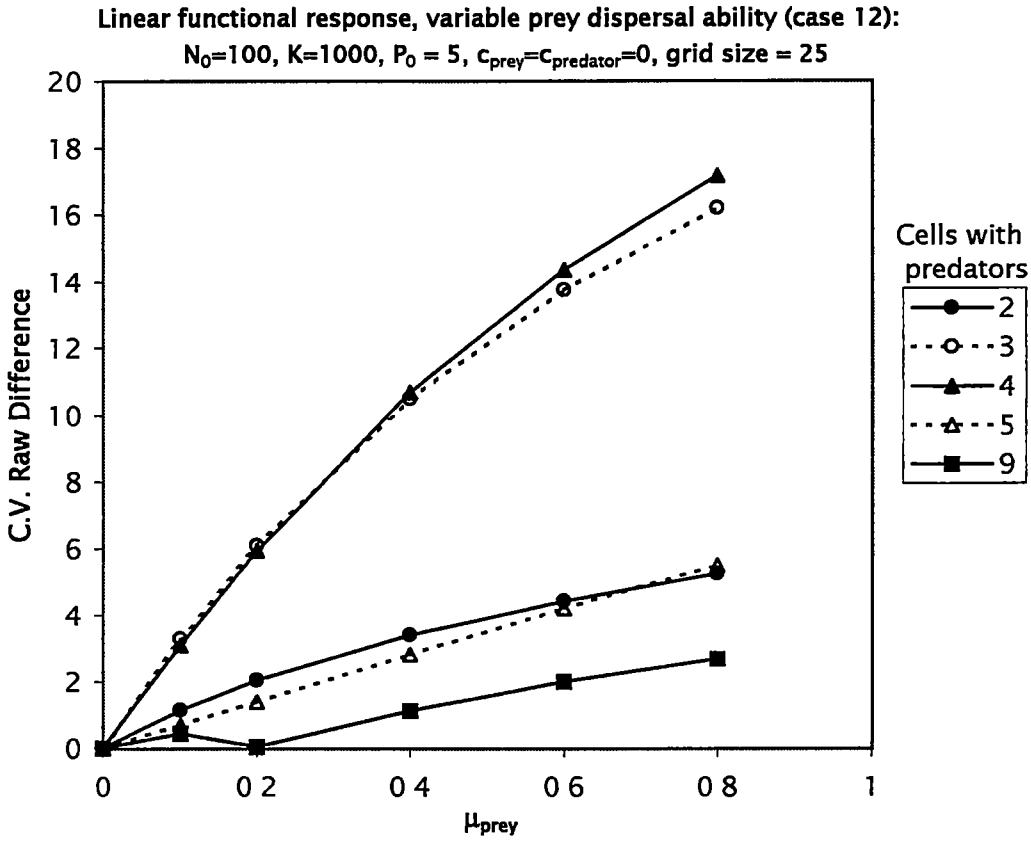


FIGURE 33. Relation of prey dispersal ability (μ_{prey}) with logistic prey growth and linear functional response (Table 1, case 12) to the coefficient of variation (CV) for the raw difference (RD) among different predator spatial distributions (linear, clumped, spread, and very spread) for a particular number of cells with predators on a 49 cell grid. Each of the five symbols gives the CV among the following predator distributions (see Fig 2): i) 2 clumped, spread; ii) 3 linear, spread, very spread, on boundary; iii) 4 clumped, spread, very spread, on boundary, iv) 5 linear, spread, very spread; and v) 9 clumped, spread, very spread. Patterns for the coefficient of variation in CI, PI, and DI were qualitatively similar to that of RD.

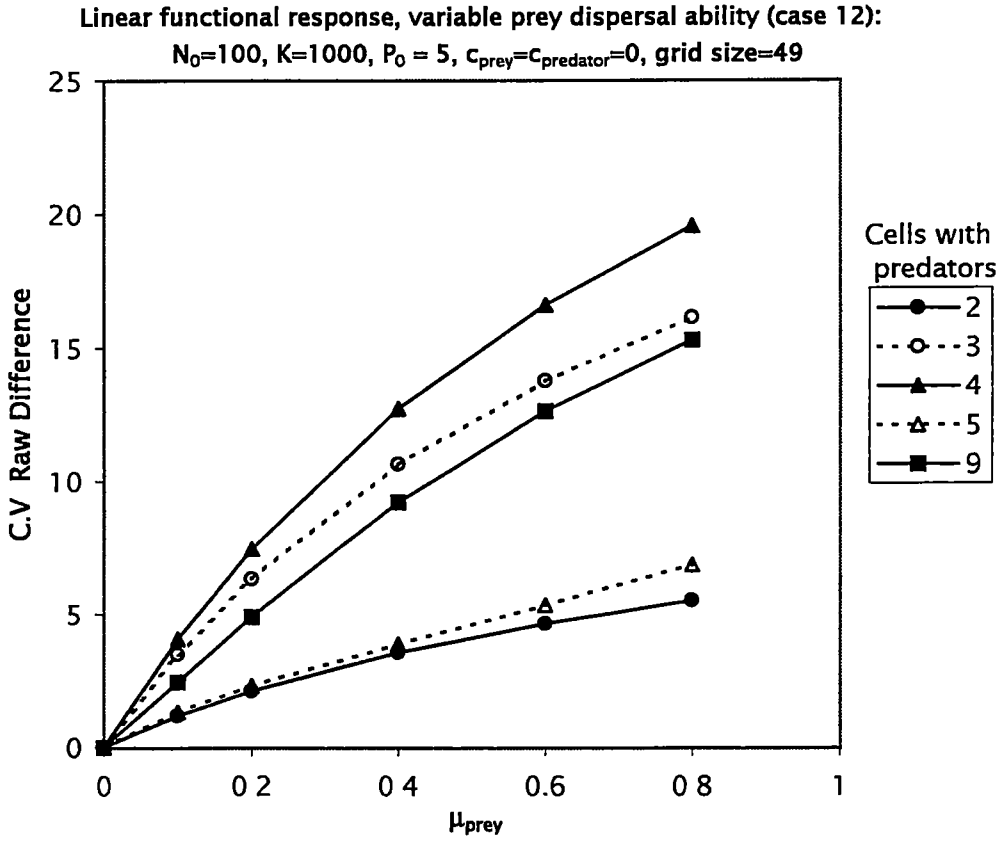


FIGURE 34. Average raw difference (RD) among different prey dispersal abilities (μ_{prey}) for each of the predator distributions and number of cells occupied by predators (Fig. 2) in (a) 25 cell grid and (b) 49 cell grid. Prey growth was logistic and predator functional response was linear (case 12). Patterns among predator distributions for RD were similar to those for CI, PI, and DI.

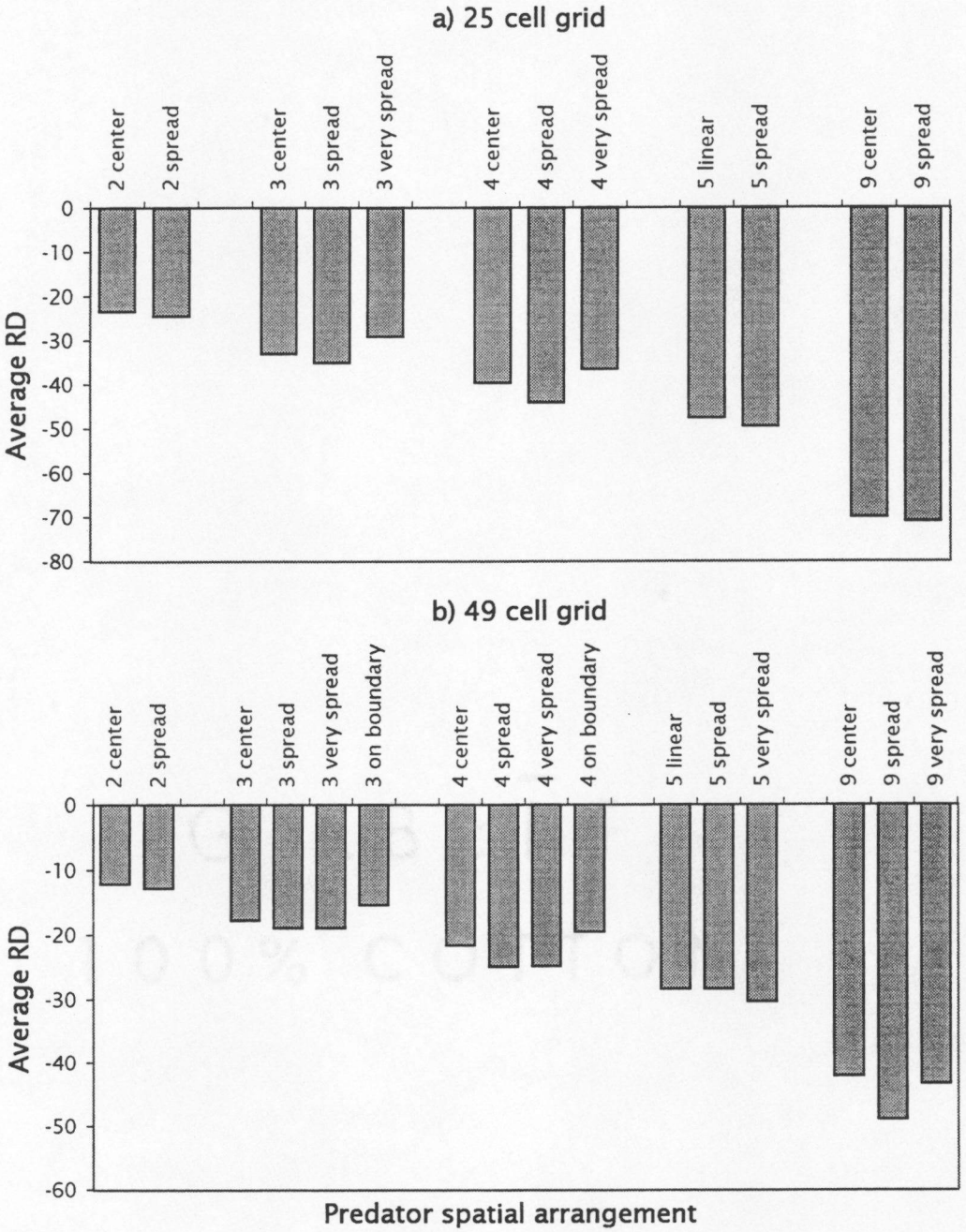


FIGURE 35. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 25 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 13 (Table 1), where prey growth was logistic, predator interference was allowed ($c_{predator}$=0.1), prey dispersal ability ranged (μ_{prey}) from 0 to 0.8, and initial average prey density (N_0), prey carrying capacity (K), and average predator density (P_0) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different initial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

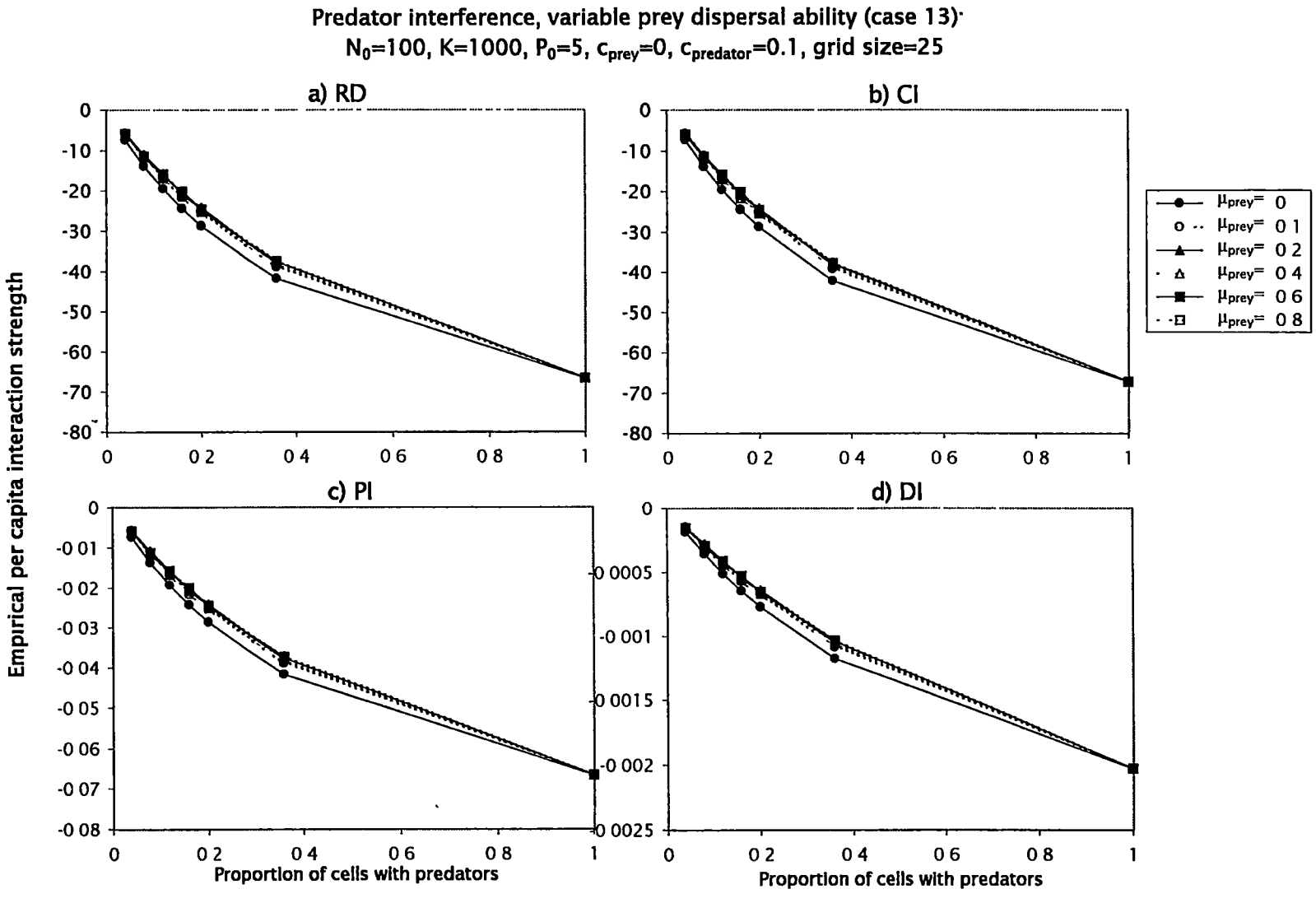

Predator interference, variable prey dispersal ability (case 13)
N0=100, K=1000, P0=5, cprey=0, cpredator=0.1, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Proportion of cells with predators
Proportion of cells with predators
μprey= 0
μprey= 0 1
μprey= 0 2
μprey= 0 4
μprey= 0 6
μprey= 0 8

FIGURE 36. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 49 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 13 (Table 1), where prey growth was logistic, predator interference was allowed ($c_{predator}$=0.1), prey dispersal ability ranged (μ_{prey}) from 0 to 0.8, and initial average prey density (N_0), prey carrying capacity (K), and average predator density (P_0) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig 2).

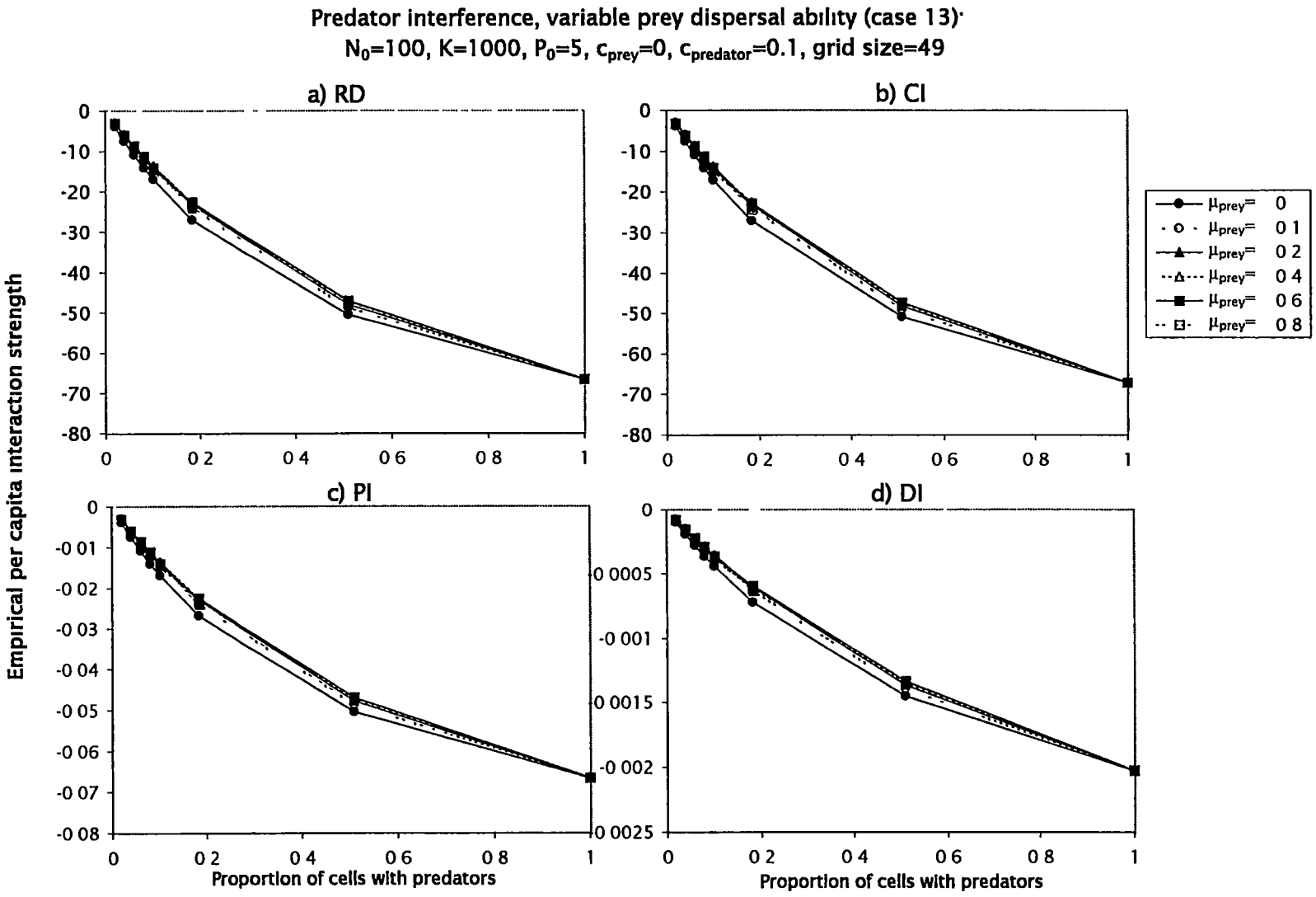

Predator interference, variable prey dispersal ability (case 13)
N0=100, K=1000, P0=5, cprey=0, cpredator=0.1, grid size=49
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Proportion of cells with predators
Proportion of cells with predators
μprey= 0
μprey= 0 1
μprey= 0 2
μprey= 0 4
μprey= 0 6
μprey= 0 8

FIGURE 37. Relation of prey dispersal ability (μ_{prey}) with logistic prey growth and predator interference (Table 1; case 13) to the coefficient of variation (CV) for the raw difference (RD) among different predator spatial distributions (linear, clumped, spread, and very spread) for a particular number of cells with predators on a 25 cell grid. Each of the five symbols gives the CV among the following predator distributions (see Fig. 2) i) 2 clumped, spread; ii) 3 linear, spread, very spread; iii) 4 clumped, spread, very spread; iv) 5 linear, spread; and v) 9 clumped, spread Patterns for the coefficient of variation in CI, PI, and DI were qualitatively similar to that of RD.

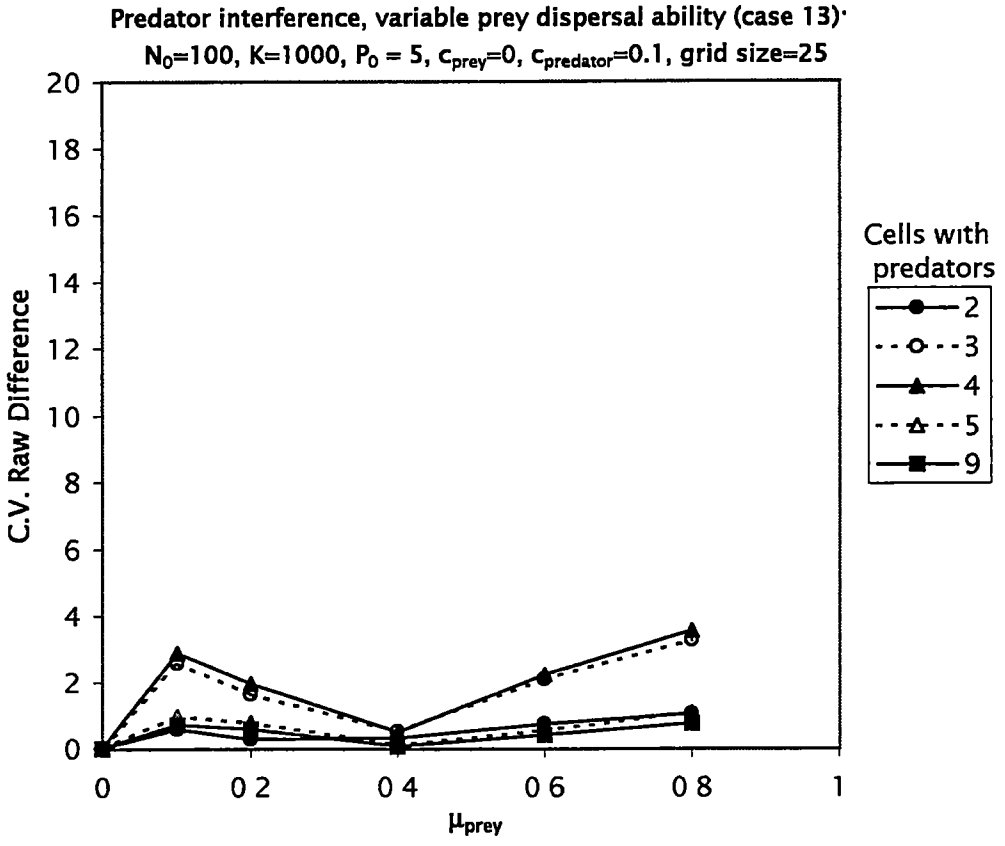


FIGURE 38 Relation of prey dispersal ability (μ_{prey}) with logistic prey growth and predator interference (Table1; case 13) to the coefficient of variation (CV) for the raw difference (RD) among different predator spatial distributions (linear, clumped, spread, and very spread) for a particular number of cells with predators on a 49 cell grid. Each of the five symbols gives the CV among the following predator distributions (see Fig. 2): i) 2 clumped, spread; ii) 3 linear, spread, very spread, on boundary; iii) 4 clumped, spread, very spread, on boundary; iv) 5 linear, spread, very spread; and v) 9 clumped, spread, very spread. Patterns for the coefficient of variation in CI, PI, and DI were qualitatively similar to that of RD.

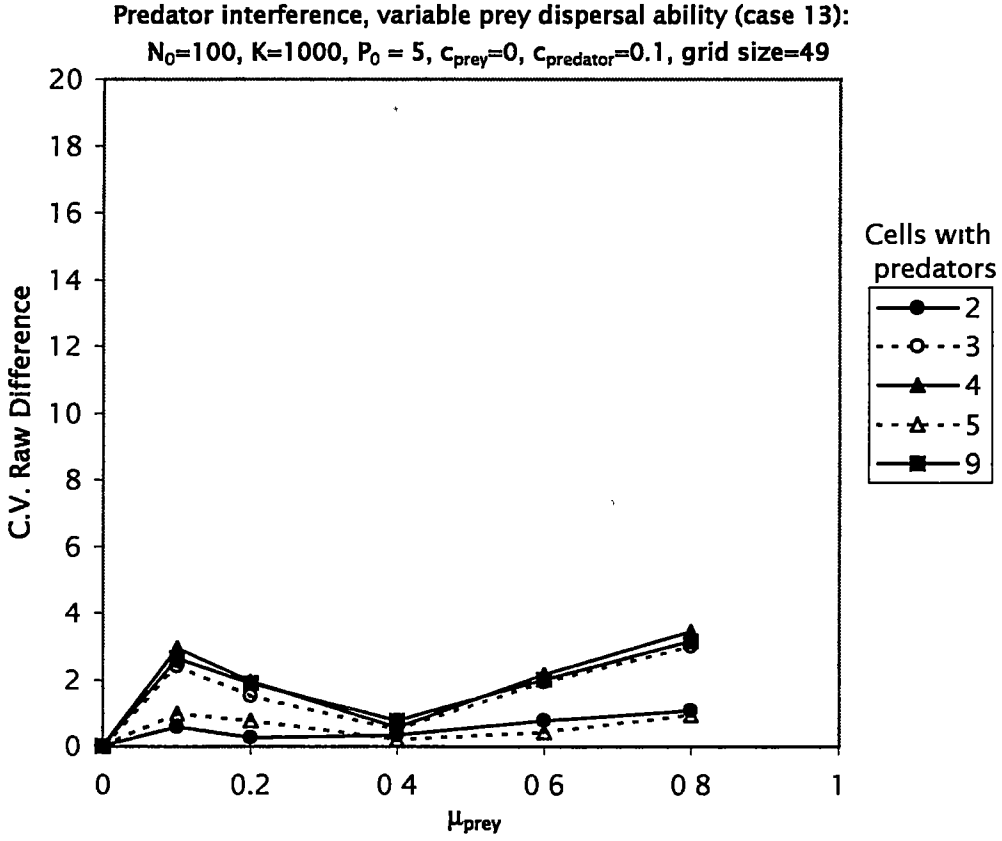


FIGURE 39. Temporal trajectories of the per capita interaction strength for each of the different predator spatial arrangements (Fig. 2) on a 25 cell grid, as measured by the different indices, estimated from simulations with vs. without predators, for case 14 (Table 1), where prey growth was logistic, predator functional response was a saturating function of prey density (c_{prey}=0.005), and average predator density (P_0) was 5. Average initial prey density (N_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. Temporal trajectories for μ_{prey} ranging from 0 to 0.6 were qualitatively similar to μ_{prey}=0.8, although the order of interaction strengths from least to most negative varied. Temporal trajectories for μ_{prey}=0.2 are shown in Fig. 11; other μ_{prey} are not shown. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different predator spatial arrangements; some lines may overlap where interaction strengths were similar.

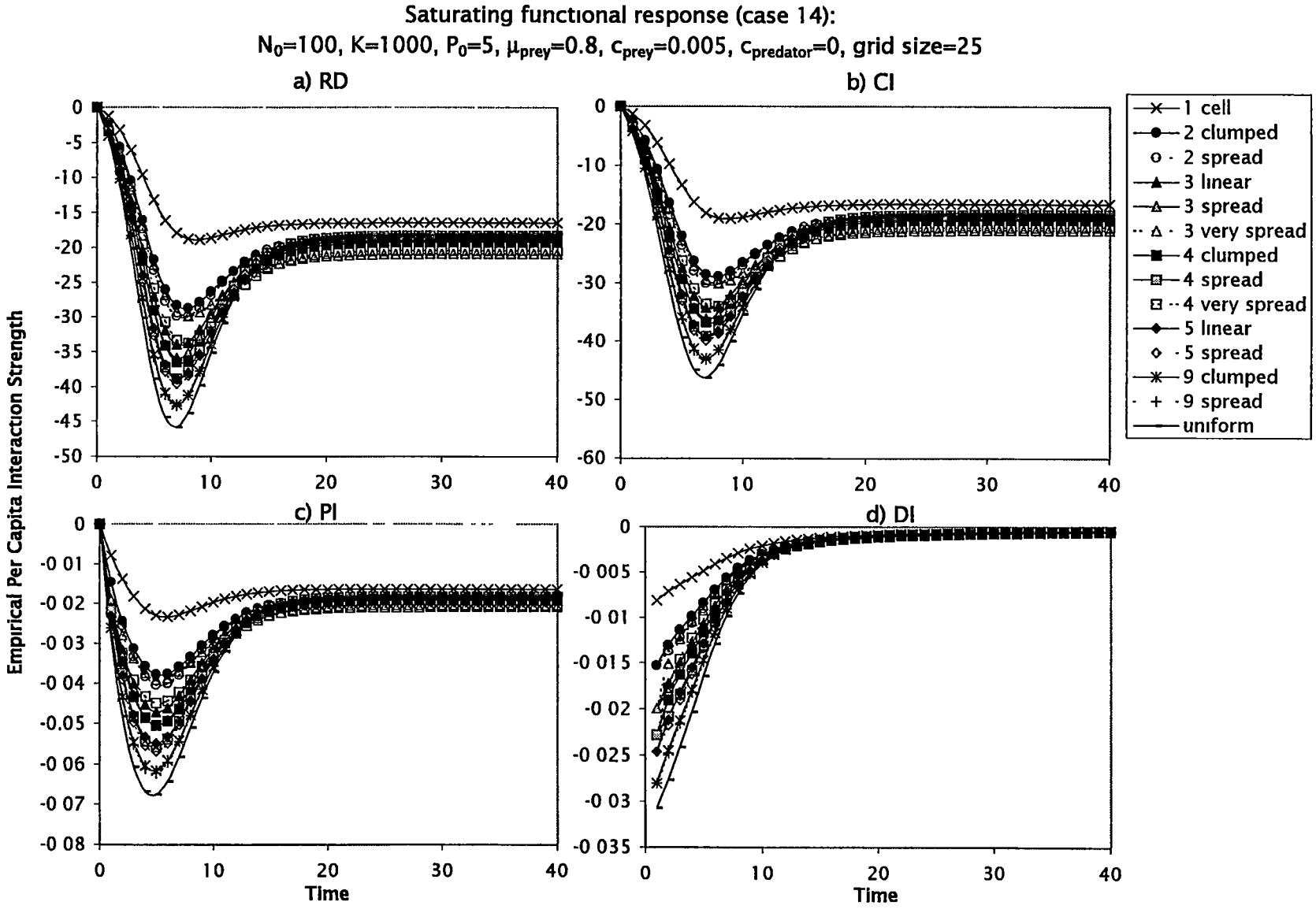

Saturating functional response (case 14):
N0=100, K=1000, P0=5, μprey=0.8, cprey=0.005, cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical Per Capita Interaction Strength
Time
Time
1 cell
2 clumped
2 spread
3 linear
3 spread
3 very spread
4 clumped
4 spread
4 very spread
5 linear
5 spread
9 clumped
9 spread
uniform

FIGURE 40. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 25 cell grid, quantified as proportion of grid cells occupied by predators, as measured by the different indices, estimated from simulations with vs. without predators, for case 13 (Table 1), where prey growth was logistic, predator functional response was a saturating function of prey density (c_{prey}=0.005), prey dispersal ability ranged (μ_{prey}) from 0 to 0.8, and initial average prey density (N_0), prey carrying capacity (K), and average predator density (P_0) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all five lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

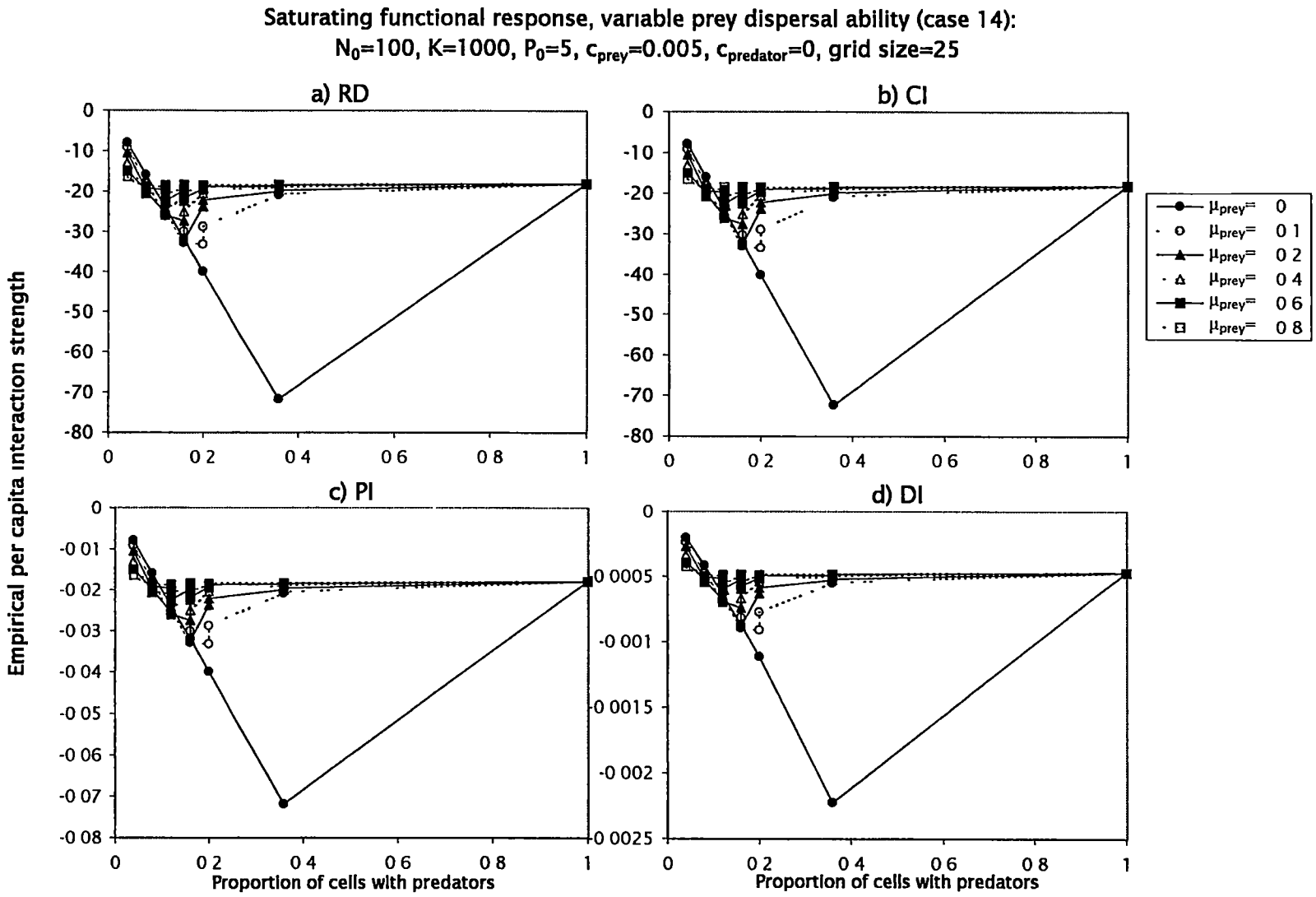

Saturating functional response, variable prey dispersal ability (case 14):
N_0=100, K=1000, P_0=5, c_{prey}=0.005, $c_{predator}$=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Proportion of cells with predators
Proportion of cells with predators
μ_{prey}= 0
μ_{prey}= 0 1
μ_{prey}= 0 2
μ_{prey}= 0 4
μ_{prey}= 0 6
μ_{prey}= 0 8

FIGURE 41 Relation of prey dispersal ability (μ_{prey}) with logistic prey growth and saturating predator functional response (Table1; case 14) to the coefficient of variation (CV) for the raw difference (RD) among different predator spatial distributions (linear, clumped, spread, and very spread) for a particular number of cells with predators. Each of the five symbols gives the CV among the following predator distributions (see Fig. 2): i) 2 clumped, spread; ii) 3 linear, spread, very spread; iii) 4 clumped, spread, very spread; iv) 5 linear, spread; and v) 9 clumped, spread. Patterns for the coefficient of variation in CI, PI, and DI were qualitatively similar to that of RD.

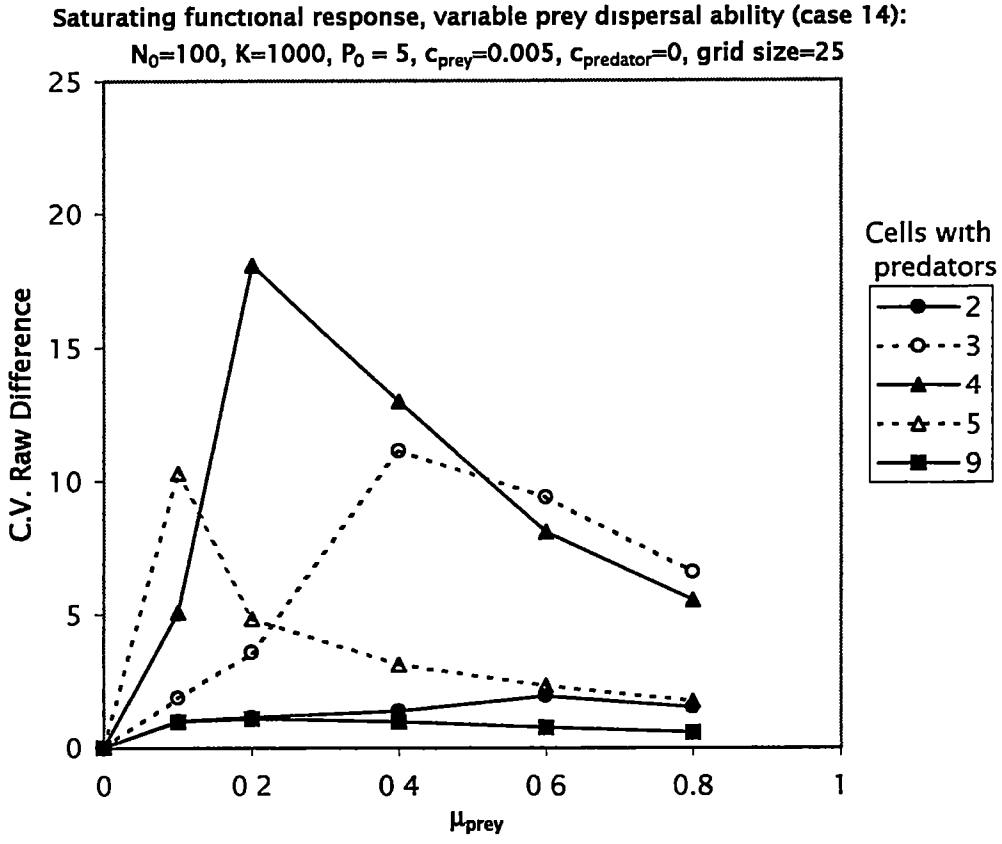


FIGURE 42. Average raw difference (RD) among different prey dispersal abilities (μ_{prey} ranging from 0.4 to 0.8) for each of the predator distributions and number of cells occupied by predators on a 25 cell grid (Fig. 2) where prey growth was logistic and predator functional response was a saturating function of prey density (Table 1; case 14). Patterns among predator distributions for RD were similar to those for CI, PI, and DI.

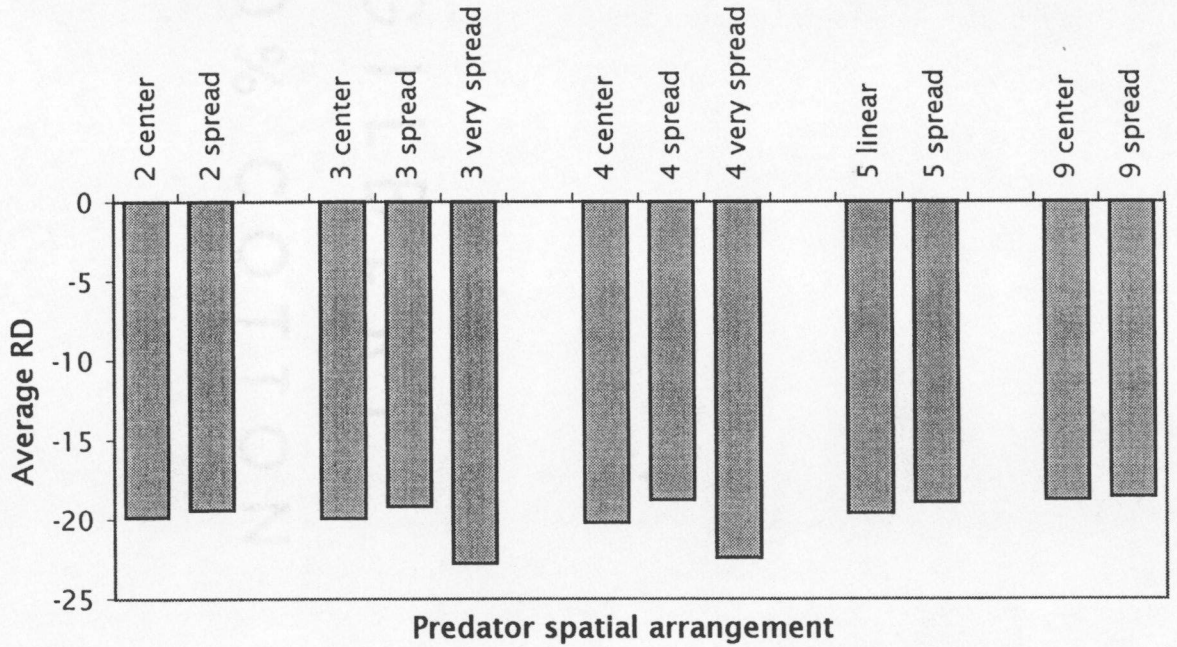


FIGURE 43. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2) on a 25 cell grid, quantified by local predator density in a single predator occupied cell (total predator number in spatial grid/number of cells occupied by predators), as measured by the different indices, estimated from simulations with vs. without predators, where prey growth was logistic, predator functional response was linear (c_{prey}=$c_{predator}$=0), average predator density (P_0) ranged from 1 to 10, and initial average prey density (N_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different intial average prey densities; where only one line is visible, all three lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

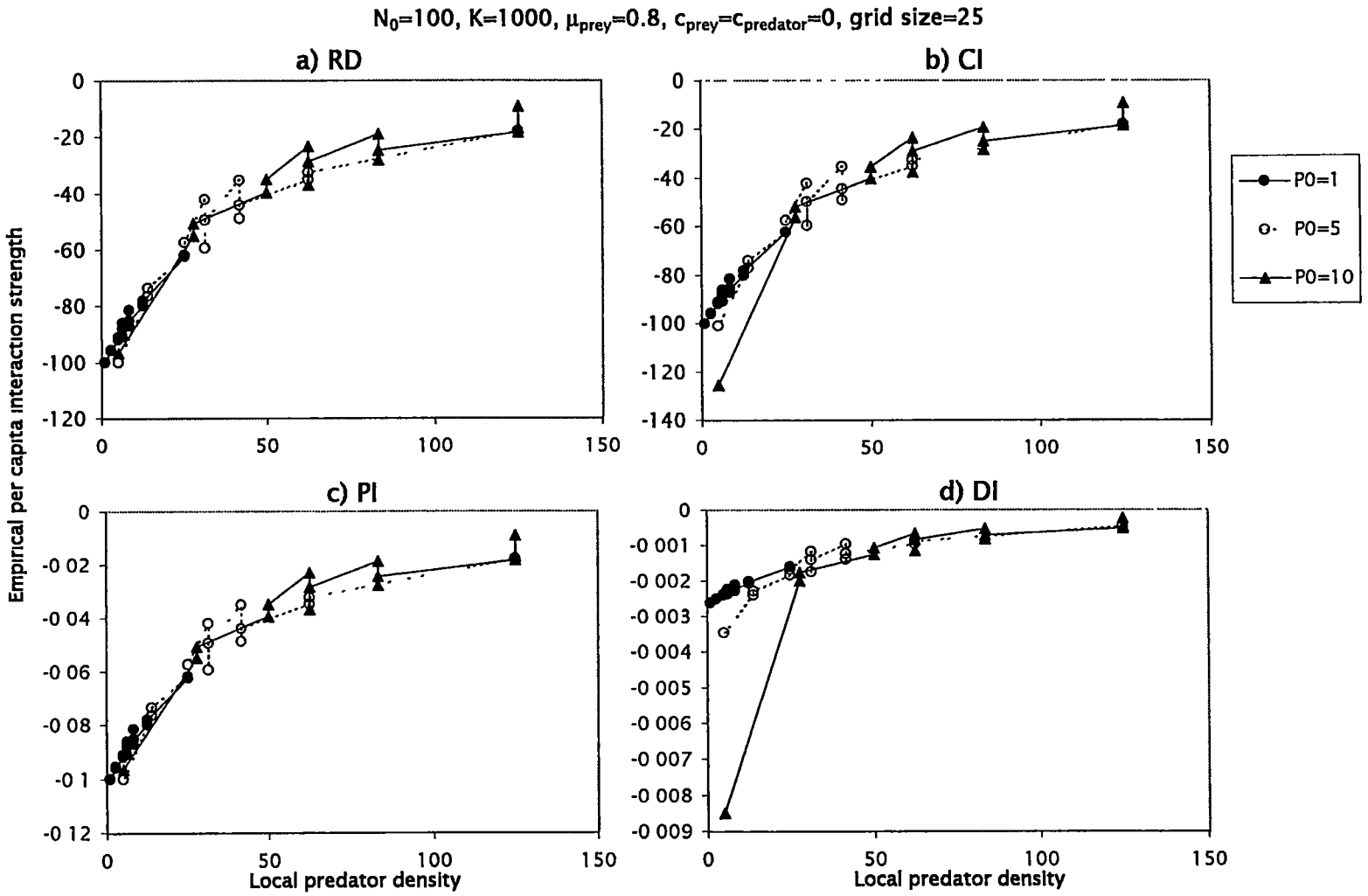

N0=100, K=1000, μprey=0.8, cprey=cpredator=0, grid size=25
a) RD
b) CI
c) PI
d) DI
Empirical per capita interaction strength
Local predator density
Local predator density
P0=1
P0=5
P0=10

FIGURE 44. Per capita interaction strengths at 40 time steps for different predator spatial arrangements (Fig. 2), quantified by local predator density in a single predator occupied cell (total predator number in spatial grid/number of cells occupied by predators), on a 9 or 25 cell grid, surrounded by a prey matrix 0, 1, or 2 cells wide (cases 15, 16; Table 1). Interaction strength indices were estimated from simulations with vs. without predators on the 9 or 25 cell grid. Prey growth was logistic, predator functional response was linear ($c_{prey}=c_{predator}=0$), and average predator density (P_0), initial average prey density (N_0), prey dispersal ability (μ_{prey}), and prey carrying capacity (K) were held constant across all runs. (a) RD, Raw difference, (b) CI, Community Importance, (c) PI, Paine's Index, and (d) Dynamic Index. The different lines represent different initial average prey densities; where only one line is visible, lines overlap. Multiple points for a particular proportion of grid cells occupied by predators indicate interaction strengths for different predator distributions: clumped, linear, spread, or very spread (Fig. 2).

Linear functional response, variable number of prey cells surrounding grid (cases 15, 16):
N_0=100, K=1000, P_0=5, μ_{prey}=0.2, c_{prey}=$c_{predator}$=0, grid size=9, 25

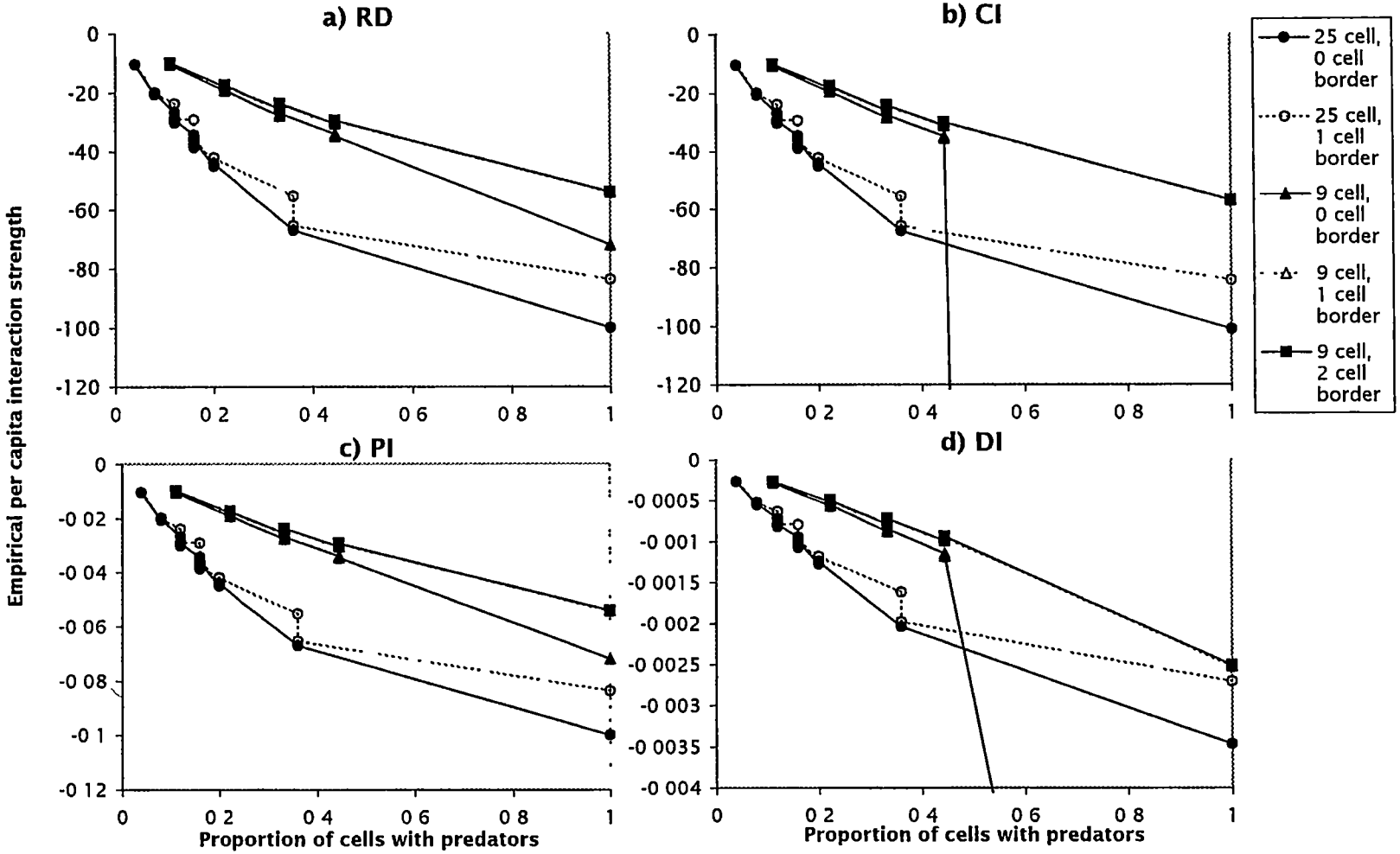
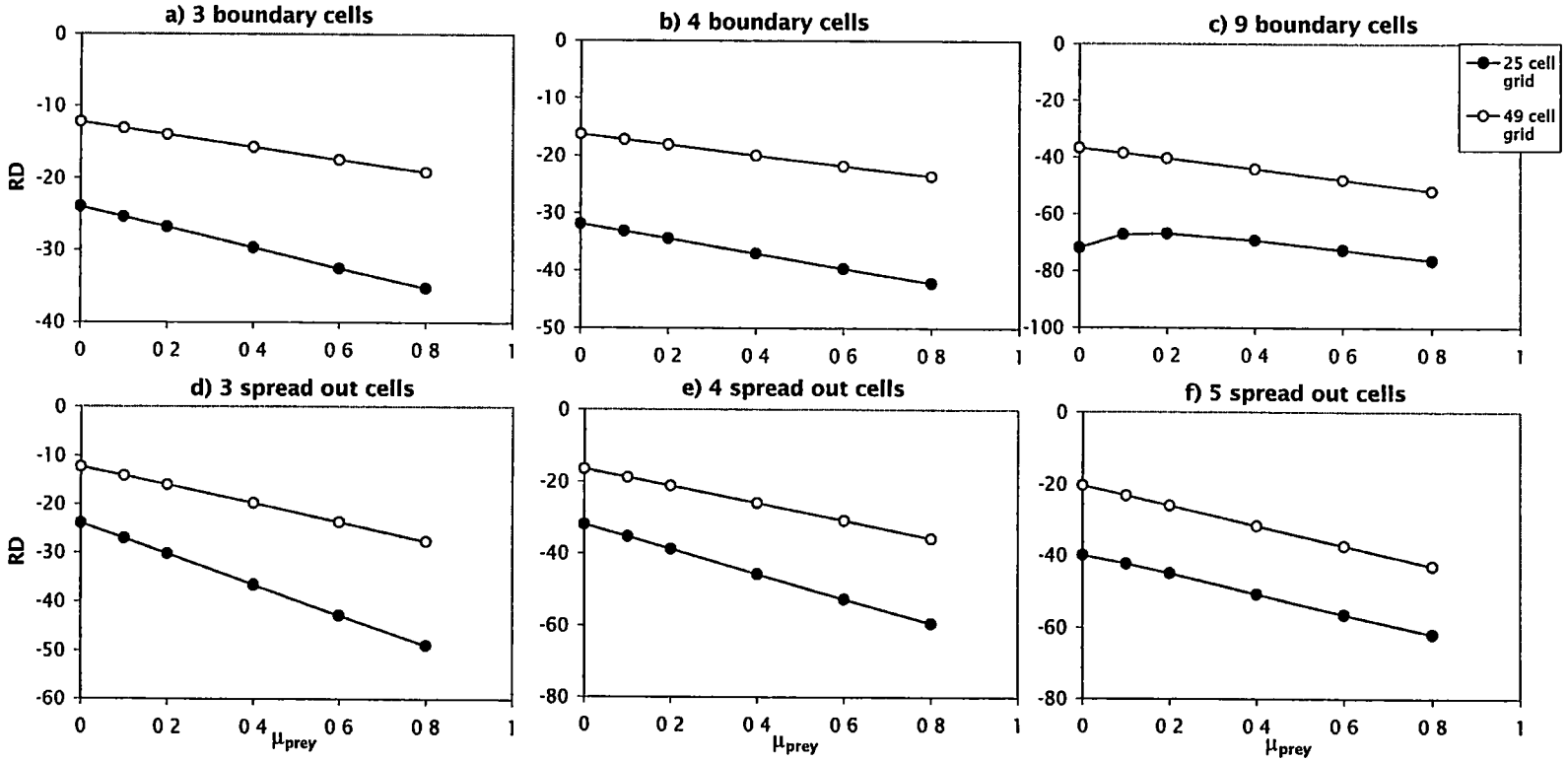


FIGURE 45. Raw difference (RD) for different predator spatial arrangements in case 12 (Table 1) in which the distance between predator occupied cells and prey movement were increased. Predators were confined to (a) 3 boundary cells (Figs 2f and 2p), (b) 4 boundary cells (Figs. 2i and 2q), (c) 9 boundary cells (Figs. 2m and 2s), (d) 3 spread out cells (Figs. 2e and 2f), (e) 4 spread out cells (Figs. 2h and 2i), or (f) 5 spread out cells (Figs. 2k and 2r), on grids of varying spatial extents. As the spatial extent increased from 25 to 49 cells, the distance between predator cells increased from 3 to 5 cells for predators occupying 3 or 4 boundary cells, 1 to 2 cells for predators occupying 9 spread out cells, and 1 to 3 for predators occupying 3, 4, or 5 spread out cells. For each predator distribution and spatial extent, prey movement varied from μ_{prey}=0.0 to 0 8 Patterns for CI, PI, and DI were qualitatively similar to those of RD.



VITA

Susan Harrell was born in Fort Worth, Texas on July 21, 1975. She attended schools in Burleson, TX and Amarillo, TX before completing high school in Albuquerque, NM in May 1993. She entered Texas Tech University, Lubbock, TX in August 1993, where she received a Howard Hughes Medical Institute Undergraduate Fellowship in Ecology. She graduated in December 1996 with a Bachelor of Science in Mathematics and minor in Biological Sciences. She spent the next four months as a Science and Engineering Research Semester Fellow at Oak Ridge National Labs, Oak Ridge, TN, and then spent three months working as a Texas Tech Tropical Ecology Fellow at El Verde Field Station, Puerto Rico. In August 1997, she entered the University of Tennessee, Knoxville to pursue a Master of Science in Mathematical Ecology. The master's degree was received August 2000. She has been accepted into the Ph.D. program in Ecology and Evolutionary Biology at the University of Chicago, Chicago, Illinois beginning September 2000.