Modelling the dynamics of complex food webs

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3.1 Introduction

The world is currently facing losses of biodiversity and habitats, species invasions, climate change, groundwater depletion and other anthropogenic perturbations that are resulting in the drastic reorganization of many ecosystems. In order to understand, predict and mitigate such reorganizations, which can severely affect ecosystem services (Daily 1997) that humans depend on such as water supply and purification and crop pollination, researchers need to broaden their focus from particular types of species to whole ecosystems. Ecological network research provides a very compelling framework for addressing the complexity of species interactions with each other and the environment. For example, the effects of any stressor – abiotic or biotic, natural or anthropogenic – on one population can cascade through ecological networks as a result of direct and indirect interactions, potentially affecting any other population in the same ecosystem. While much research has focused on direct effects between species or their populations, empirical and modelling studies have shown that effects due to indirect species interactions can be as important as direct effects in driving outcomes (Abrams *et al.* 1995; Menge 1997; Yodzis 2000). In fact, indirect effects can be stronger than the direct effects of a stressor, potentially greatly modifying the overall outcomes for population abundances in the face of extinctions (Ives and Cardinale 2004). Network analysis and modelling provide approaches for quantifying and assessing both direct and indirect effects. In general, determining the interplay among network structure, network dynamics and various aspects of stability such as persistence, robustness and resilience in complex 'real-world' networks is one of the greatest current challenges in the natural and social sciences, and it represents an exciting and dramatically expanding area of cross-disciplinary inquiry (Strogatz 2001).

3.2 Simple trophic interaction modules and population dynamics

While there are many types of interactions that species can have with each other, trophic (feeding) interactions are ubiquitous, are central to both ecological and evolutionary dynamics and are relatively easily observed, defined, quantified and modelled compared with other kinds of interactions. Within ecology, food web research, the study of networks of trophic interactions, represents a long tradition of both empirical and theoretical network analysis (Elton 1933; Lindeman 1942; MacArthur 1955; May 1973; Cohen *et al.* 1990; Pimm *et al.* 1991; see review by Egerton 2007). Ideally, food web research seeks to identify, analyse and model feeding interactions among whole communities of taxa including plants, bacteria, fungi, invertebrates and vertebrates, with feeding links representing transfers of biomass via various trophic interactions including detritivory, herbivory, predation, cannibalism and parasitism. A great deal of food web research, starting in the mid-1970s, has focused on various aspects of how such networks are structured (see review by Dunne 2006), with emerging strong empirical and model-based

evidence that food webs from different habitats have similar characteristic topologies (Williams and Martinez 2000; Camacho *et al.* 2002; Dunne *et al.* 2002, 2004; Milo *et al.* 2002; Stouffer *et al.* 2005, 2006, 2007; see also Chapter 1).

However, food webs are inherently dynamical systems, since feeding interactions involve variable flows of biomass among species whose population densities are changing over time in response to direct and indirect interactions. Because it is difficult to compile detailed, long-term empirical datasets for dynamics of two or more interacting species, much research on species interaction dynamics relies on modelling. Many modelling studies of trophic dynamics have used analytically tractable approaches to explore predator–prey or parasite–host interactions (Yodzis and Innes 1992; Weitz and Levin 2006) or small modules of interacting taxa (McCann *et al.* 1998; Fussmann and Heber 2002), generally ignoring all but the most simple of possible network structures. In natural ecosystems, such interaction dyads or modules are embedded in diverse, complex food webs, where many additional taxa and their direct and indirect effects can play important roles for both the stability of focal species and the stability of the broader community. Therefore, it is critically important to ask whether knowledge about population dynamics obtained in small interaction modules (Yodzis and Innes 1992; McCann and Yodzis 1994; McCann *et al.* 1998; Fussmann and Heber 2002; Weitz and Levin 2006) applies to population dynamics in more realistically complex food webs.

Analyses of such modules suggest that every additional feeding link between the species may change the population dynamics dramatically. For instance, the dynamics of three populations in a tri-trophic food chain (Fig. 3.1a) can be stabilized or destabilized by an additional link from the top species to the basal species (McCann and Hastings 1997; Vandermeer 2006). By convention, this module (Fig. 3.1b) is termed an omnivory module (or intra-guild predation module). Depending on the relative strength of the links this module represents an intermediate stage between a tri-trophic food chain (in which the top species does not consume the basal species) and an exploitative competition module (in which the top species does not consume
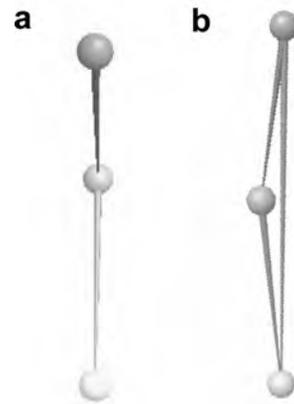

Figure 3.1 Structure of food web modules. (a) Tri-trophic food chain; (b) omnivory or intra-guild predation module.

the intermediate species). Now, omnivory as the stage between these extremes can stabilize population dynamics by either eliminating chaotic dynamics or bounding the minima of the population densities away from zero (McCann and Hastings 1997). However, opposite results can be obtained with different parameters for population traits (Vandermeer 2006). Generally, omnivory can stabilize the population dynamics if the tri-trophic food chain and the exploitative competition module at the extremes of the gradient are unstable, whereas omnivory should destabilize the system if the modules at the extremes of the gradient are stable (Vandermeer 2006). Furthermore, the consequences of omnivory in a comparable simple experimental system are highly dependent on nutrient enrichment, since coexistence of both consumers is restricted to intermediate nutrient saturations (Diehl and Feissel 2001). Extending the size of the food web modules beyond three populations, Fussmann and Heber (2002) demonstrated that the frequency of chaotic dynamics increases with the number of trophic levels, but decreases with other structural properties that cause higher food web complexity. Interestingly, these results indicate that population stability might increase or decrease with food web complexity, depending on which process dominates in a particular food web. These studies have emphasized the critically important roles of network complexity and the distribution of interaction strengths across feeding links in determining

population dynamics. However, it remains to be seen (1) whether our understanding of population dynamics in small modules can be scaled up to complex food webs and (2) how global characteristics of complex food webs such as connectance (a measure of link richness – the probability that any two species will interact with each other; see Chapter 1) affect population dynamics. In the next section, we describe an approach using keystone species that addresses the first question.

3.3 Scaling up keystone effects in complex food webs

In keystone species modules, a keystone consumer of a competitively dominant basal species facilitates the coexistence of competitively subordinate basal species (Fig. 3.2). When the keystone species is experimentally removed or goes locally extinct, competition can lead to extinction of the subordinate basal species. Such facilitation of basal species co-

Figure 3.2 Keystone consumer in (a) a small module and (b) a complex food web. See plate 2.

existence by a keystone consumer was first described for the starfish *Pisaster ochraceus* that preferentially consumes the competitively dominant mussel *Mytilius californianus*, and thereby facilitates the coexistence of a diverse community of basal species that are competitively subordinate to the mussel (Paine 1966, 1974). Thus, the starfish has a positive effect on the biomass density of most species in the intertidal food web (i.e. the biomass density of most species is higher when the starfish is present than when it is absent). This facilitation by *Pisaster* was termed a 'keystone effect'. Similar keystone effects of other consumer species have subsequently been documented for many other ecosystems (Power *et al.* 1996), which suggests a broad generality of this phenomenon. However, the strength of the keystone effect varies dramatically between years and sites within ecosystems (Paine 1980; Menge *et al.* 1994; Berlow 1999). Analyses of keystone modules have shown that keystone effects vary substantially with the presence or absence of peripheral (non-keystone) species and links (Brose *et al.* 2005). This suggests that keystone effects in complex food webs (Fig. 3.2b) might be highly context dependent.

Systematic simulation analyses of complex food webs have revealed surprisingly simple determinants of keystone effects (Brose *et al.* 2005). Generally, distant effects of the global network structure or effects of populations that are more than two degrees (trophic links) separated from the keystone module are buffered by the network structure. Most likely, the multiple pathways between populations in complex food webs are characterized by effects of different signs that cancel each other out. Thus, effects between two species over pathways longer than two degrees often cancel each other out, and only effects over one or two degrees of separation that dominate in food webs (Williams *et al.* 2002) are not balanced by other interaction pathways of opposite sign and could systematically vary the strength of the keystone effect. These results suggest that effects within keystone modules that are embedded in complex food webs are affected by other populations within a 'local interaction sphere' of influence, which includes effects of non-keystone species that are separated by one or two links from the keystone module (Brose *et al.*
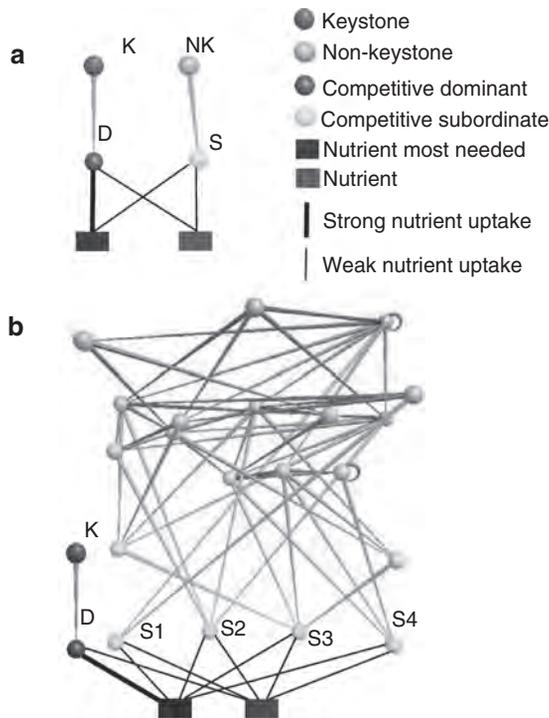
2005). If these results generalize to other types of modules such as omnivory modules, population dynamics in natural food webs may be determined by local interaction spheres that are larger than the classic modules, but smaller than entire complex food webs.

3.4 Diversity/complexity–stability relationships

Much of the research on food web dynamics in model systems with more than two taxa has been orientated around the classic (May 1972) and enduring (McCann 2000) debate on how diversity and complexity of communities affect food web stability. In the first half of the 20th century, many ecologists believed that natural communities develop into stable systems through successional dynamics. Aspects of this belief developed into the notion that complex communities are more stable than simple ones (Odum 1953; MacArthur 1955; Elton 1958; Hutchinson 1959). Some popular examples included the vulnerability of agricultural monocultures to calamities in contrast to the apparent stability of diverse tropical rainforests, and the higher frequency of invasions in simple island communities compared with more complex mainland communities. It was thought that a community consisting of species with multiple consumers would have fewer invasions and pest outbreaks than communities of species with fewer consumers. This was stated in a general theoretical way by MacArthur (1955), who hypothesized that 'a large number of paths through each species is necessary to reduce the effects of overpopulation of one species'. MacArthur concluded that 'stability increases as the number of links increases' and that stability is easier to achieve in more diverse assemblages of species, thus linking community stability with both increased trophic links and increased numbers of species. Other types of theoretical considerations emerged to support the positive complexity–stability relationship. For example, Elton (1958) argued that simple predator–prey models reveal their *lack* of stability in the oscillatory behaviour they exhibit, although he failed to compare them with multispecies models (May 1973). The notion that 'diversity and complexity beget stability',

which already had great intuitive appeal as well as the weight of history behind it, was thus accorded a gloss of theoretical rigor (e.g. a 'formal proof' according to Hutchinson 1959), and took on the patina of conventional wisdom by the late 1950s.

The concept that complexity implies stability, as a theoretical generality, was explicitly and rigorously challenged by the analytical work of May (1972, 1973), a physicist by training and ecologist by inclination. He used local stability analyses of randomly assembled community matrices to mathematically demonstrate that network stability decreases with complexity. In particular, he found that more diverse systems, compared with less diverse systems, will tend to sharply transition from stable to unstable behaviour as the number of species, the connectance *or* the average interaction strength increase beyond a critical value. May's analytical results and his conclusion that 'in general mathematical models of multispecies communities, complexity tends to beget instability' (May 2001, p. 74) turned earlier ecological 'intuition' on its head and instigated a dramatic shift and refocusing of theoretical ecology. His results left many empirical ecologists wondering how the astonishing diversity and complexity they observed in natural communities could persist, even though May himself insisted there was no paradox. May framed a central challenge for ecological research this way: 'In short, there is no comfortable theorem assuring that increasing diversity and complexity beget enhanced community stability; rather, as a mathematical generality, the opposite is true. The task, therefore, is to elucidate the devious strategies which make for stability in enduring natural systems' (May 2001, p. 174).

3.5 Stability of complex food webs: community matrices

Despite methodological criticism of May's methodology (e.g. Cohen and Newman 1984) much subsequent work related to food webs was devoted to finding network structures, species' strategies and dynamical characteristics that were consistent with May's theorem or that would allow complex communities to be stable or persist. May (1972,

1973) used random matrices of interactions for his analyses, which yield random network structures ('who eats whom') and random distributions of traits and interaction strengths ('how much is eaten') across the populations and links in the networks. In natural food webs, however, neither the matrices of interactions nor the distributions of interaction strengths are random. Systematic patterns of low assimilation efficiencies, strong self-regulation (negative effects of a species on its own biomass) or donor control of biomasses can cause positive complexity–stability relationships (DeAngelis 1975). Subsequent analyses demonstrated that non-random empirical network structures of natural food webs are more dynamically stable than random networks (Yodzis 1981), suggesting that natural food webs possess a topology that increases the stability of the population dynamics.

Extending the approach of adding empirical realism to stability analyses, de Ruiter *et al.* (1995) parameterized May's general community matrix model with empirical food web structures and interaction strengths among the species. In their empirical data, they found a pattern of strong top-down effects of consumers on their resources at lower trophic levels in food webs and strong bottom-up effects of resources on their consumers at higher trophic levels. Adding empirical interaction strength patterns to the community matrices increased their local stability in comparison with matrices with random interaction strength values (de Ruiter *et al.* 1995). Most importantly, these results demonstrated that natural food web structures as well as the distribution of interaction strengths within those structures contribute to an increased local stability of the corresponding community matrices. Neutel *et al.* (2002) explained this finding with results that showed that weak interactions are concentrated in long loops. In their analysis, a loop is a pathway of interactions from a certain species through the web back to the same species, without visiting other species more than once. They defined loop weight as the geometric mean of the interaction strengths in the loop and showed that loop weight decreases with loop length. Again, when applied to the community matrix, this empirically documented pattern of in-

teraction strength distributions increased its local stability in comparison with random networks (Neutel *et al.* 2002). Together, these studies demonstrate that characteristics of the distribution of links and interaction strengths within natural food webs account for their stability.

3.6 Stability of complex food webs: bioenergetic dynamics

More recent theoretical studies have extended a numerical integration approach of ordinary differential equations to complex food web models (Williams and Martinez 2004; Martinez *et al.* 2006). In this approach, the structure of the complex networks is defined by a set of simple topological models: random, cascade, niche or nested-hierarchy model food webs (Cohen *et al.* 1990; Williams and Martinez 2000; Cattin *et al.* 2004). The dynamics follow a bioenergetic model (Yodzis and Innes 1992) that defines ordinary differential equations of changes in biomass densities for each population. Numerical integration of these differential equations yields time series of the biomass evolution of each species, which allows exploration of population stability and species persistence. Similar to results from community matrix models, non-random network structure increases an aspect stability in these bioenergetic dynamics models of complex food webs: the overall persistence of species (Martinez *et al.* 2006).

One key parameter of population dynamic models is the functional response describing the *per capita* (per unit biomass of the predator) consumption rate of a predator depending on the prey biomass density. Generally the *per capita* consumption rate is zero at zero prey density and then increases with increasing prey density. According to the shape of this increase classical functional response models are characterized as (1) linear or type I, (2) hyperbolic or type II, or (3) sigmoid or type III functional responses (Fig. 3.3). The linear functional response was used in classic population dynamics studies (Lotka 1925; Volterra 1926), but lacks a biologically necessary saturation in consumption rate at high prey density. A generalized non-linear saturating functional response model (Real 1977) is
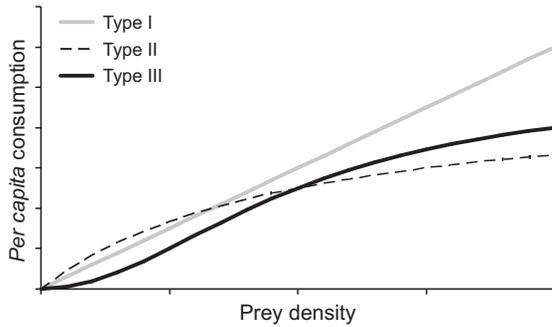
Figure 3.3 Functional responses: *per capita* consumption rates of consumers depending on prey density.

$$F(B) = \frac{cB^h}{1 + cT_hB^h} \qquad (3.1)$$

where F is the predator's consumption rate, B is prey biomass density, T_h is the handling time that includes the time a predator needs to catch, kill and ingest a unit biomass of the prey, c is a constant that describes the increase in the attack rate, a, with the prey abundance ($a \sim cB^{h-1}$), and h is the Hill coefficient that varies between 1 (type II functional response) and 2 (type III functional response). Varying the Hill exponent between 1 and 2 gradually converts a type II into a type III functional response. Williams and Martinez (2004) showed that in food webs with a type II functional response many populations are unstable and prone to extinction. Slight increases in the Hill exponent can have dramatic effects on stabilizing the dynamics of particular species, as well as overall species persistence (Williams and Martinez 2004). Additionally, Hill exponents slightly higher than 1 buffer predator–prey modules and complex food webs against the destabilizing effects of nutrient enrichment (Rall *et al*. 2008). One important stabilizing feature of this variation in functional response is the slight relaxation of consumption at low resource densities, which leads to accelerating consumption rates with increasing prey density. This yields a strong top-down pressure, which controls the prey population to low equilibrium densities (Oaten and Murdoch 1975). The relaxation of feeding at low resource density is evocative of a variety of well-documented ecological mechanisms including prey switching and refuge seeking. These types of trophic and non-trophic behaviours allow rare or low-biomass resource species to persist in both natural and model ecosystems, increasing overall community persistence.

In another approach to integrating complex structure and dynamics, and in contrast to most prior dynamical studies, Kondoh (2003, 2006) allowed consumer preferences for resources to adaptively vary. This adaptation process increases the predator preferences for prey of above-average density and decreases preferences for prey of below-average density. This adaptive foraging model yields positive complexity–stability relationships in complex food webs if (1) the fraction of adaptive foragers and (2) the speed of adaptation are sufficiently high, and (3) the number of basal species does not vary with food web complexity (Kondoh 2003, 2006). Interestingly, the process of decreasing preferences for prey of low density causes relaxation of feeding at low prey density, which is mechanistically similar to type III functional responses.

3.7 Stability of complex food webs: allometric bioenergetic dynamics

Most species' traits, T, follow close allometric power-law relationships with their body mass, M:

$$T = aM^b \qquad (3.2)$$

where a and b are constants (often b is approximately equal to ¾) and T can represent the biological rates of respiration, biomass growth or maximum consumption (Brown *et al.* 2004). These relationships can be used to parameterize population dynamic models, thus collapsing parts of the multidimensional parameter space into a body-mass axis. Moreover, natural food webs have a distinct body-mass structure of invertebrate and vertebrate predators being on geometric average roughly 10 and 100 times, respectively, larger than their prey (Brose *et al.* 2006a). Implementing theoretically and empirically supported allometric relationships in population dynamic models in complex food webs yields population dynamics models that are constrained by the body-mass structure of the food webs (Brose

et al. 2006b). In these allometric models, consumer–resource body-mass ratios define the body mass of a consumer relative to the average body mass of its resources.

Brose *et al.* (2006b) varied the consumer–resource body-mass ratios in allometric food web models systematically between 10^{-2} and 10^6, creating a gradient of food webs with predators that are 100 times smaller than their prey to food webs of predators that are 10^6 times larger than their prey (Fig. 3.4). The persistence of species in the food webs (i.e. the fraction of the initial populations that persisted during the simulations) increased with increasing body-mass ratios. Persistence is low when predators are smaller than or equal in size to their prey, but persistence increases steeply with increasing body-mass ratios (Fig. 3.4a). This increase saturates at body-mass ratios of 10 and 100 for invertebrate and vertebrate predators, respectively (Brose *et al.* 2006b), which is highly consistent with the geometric average body-mass ratios found in natural food webs (Brose *et al.* 2006a). Moreover, persistence decreases with the number of populations in the food web at low body-mass ratios, whereas it exhibits a slight increase in persistence at high body-mass ratios (Brose *et al.* 2006b).

This result confirms classic food web stability analyses (May 1972) showing negative diversity–stability relationships in random food webs, in which species are on average equally sized. But it also confirms the earlier notion of empirical ecologists (Odum 1953; MacArthur 1955; Elton 1958), who assumed positive diversity–stability relationships in natural food webs, in which species are on average 10–100 times larger than their prey. Consideration of the body-mass structure of food webs may thus reconcile lingering gaps between the perspectives of theoretical and empirical ecologists on diversity–stability relationships. It is interesting to note that, in this allometric modelling framework, a different measure of stability, the mean coefficient of variation of the species population biomasses in time in persistent webs ('population stability'), *decreases* with increasing body-size ratios until inflection points are reached that show the lowest stability, and then increases again beyond those points (Brose *et al.* 2006b). Those inflection points also correspond to the empirically observed body-size ratios (Brose *et al.* 2006a; Fig 3.4b). Thus, at intermediate body-size ratios high species persistence is coupled with low population stability. Interestingly, this demonstrated that an aspect of increased stability of the
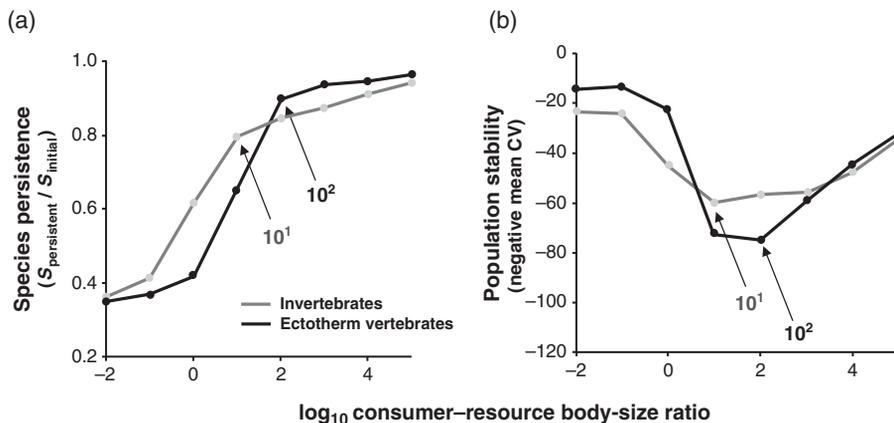

Figure 3.4 Impact of consumer–resource body-size ratios on (a) species persistence and (b) population stability depending on the species metabolic types. The inflection points for shifts to high-persistence dynamics are indicated by arrows for both curves, and those inflection points correspond to empirically observed consumer–resource body-size ratios for invertebrate dominated webs (10^1, consumers are on average 10 times larger than their resources) and ectotherm vertebrate dominated webs (10^2, consumers are on average 100 times larger than their resources). *S*, species richness; CV, coefficient of variation. Figure adapted from Brose *et al.* (2006b).

whole system (species persistence) is linked to an aspect of decreased stability of components of that system (population stability).

3.8 Future directions

Our knowledge about the structure and dynamical constraints of complex food webs has greatly improved over the last decade. The framework of dynamic food web models offers a great possibility to study the consequences of ongoing abiotic and biotic effects on natural ecosystems while including indirect effects between species. Future applications of this approach will need to further address how mechanistic knowledge gained in simple food web modules can be scaled up to predict patterns and processes in complex food webs. Local interaction spheres identified to influence the dynamics of keystone modules may help in scaling up dynamics to networks. Unravelling the factors that determine population dynamics of these local interaction spheres will be an important scientific challenge.

Implementing allometric scaling relationships in models of complex food webs has helped in understanding the processes that lead to particular distributions of interactions and network stability. Further integrations of metabolic allometry with food web research is likely to elucidate much of the constraints on structure and dynamics of complex food webs. Here, it remains particularly important to understand the allometric scaling of other model parameters such as the functional responses. Moreover, incorporating other types of consumer–resource interactions such as parasite–host links into basic food web models remains a challenge that needs to be addressed. Most likely, the framework of dynamic food web models described in this chapter will be an important backbone for future integrations of these processes into theoretical community ecology.

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Chapter 3

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Processes, Models, and Applications

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