

# Migration impacts on communities and ecosystems: empirical evidence and theoretical insights

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## 9.1 Introduction

How do migratory populations impact the communities and ecosystems that host them? In this chapter, we explore this question through a series of theoretical examples and a brief review of the available empirical evidence. We focus in particular on ungulate migrations, and more specifically on the wildebeest (*Connochaetes taurinus*) migration in the Serengeti (Box 9.1). We first identify the features of

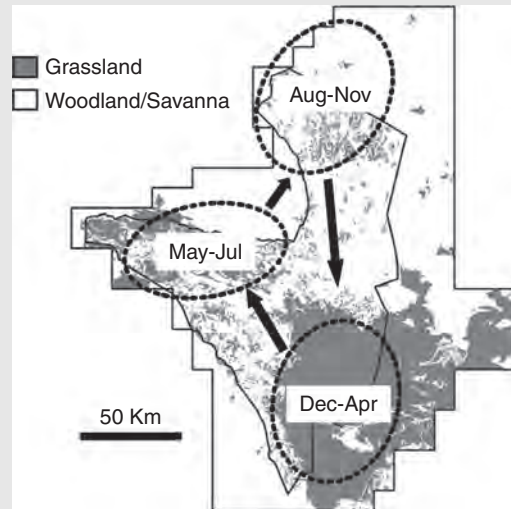
migration that distinguish it from others forms of movement, the ecosystem consequences of which (especially spatial subsidies of nutrients across ecosystem boundaries) have been studied and reviewed at length (e.g., Polis *et al.* 1997; Vanni *et al.* 2004). We then outline the various mechanisms through which migratory animals can impact ecological communities and ecosystem function, and illustrate these effects through a series of theoretical examples

### Box 9.1 The Serengeti migration as a case study

The Serengeti ecosystem is an example of a migratory system embedded in a community of resident species. Three ungulate species—wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*) and Thomson's gazelles (*Gazella thomsoni*)—undergo an annual migration between the Serengeti plains (grassland) and the woodland savannas of the western corridor and northern Serengeti, over a total area of about 25 000 km<sup>2</sup> (Fig. 9.1). The migration is driven by a marked, highly seasonal rainfall gradient, increasing from SE to NW, coupled with strong differences in soil fertility and plant nutritional content between the grassland and savanna habitats (Maddock 1979; Boone *et al.* 2006; Holdo *et al.* 2009b). Other species, including buffalo (*Syncerus caffer*) and topi (*Damaliscus lunatus*), are resident, remaining within relatively circumscribed home ranges on a year-round basis (Sinclair 1977; Murray and Brown 1993).

We illustrate with theoretical examples three facets of the Serengeti wildebeest migration: its effects on the population of a resident competitor (an example of a trophic effect impacting the herbivore community), its effects on fire and tree population dynamics (a downstream trophic effect mediated by a resource), and its effects on net primary productivity and soil fertility (a joint trophic and transport effect). In all cases, we use published models to examine how 'switching off' the migration (i.e., treating migratory

species as residents) might alter community dynamics, ecological processes such as the prevalence of fire, and ecosystem function.



**Figure 9.1** The greater Serengeti ecosystem (outer polygon) showing the Serengeti National Park (inner polygon) and a stylized depiction of the migration route followed by wildebeest, zebra and Thomson's gazelles. The two dominant habitat types (grassland, predominantly in the south-eastern plains, and woodland and savanna) are represented.

based on the Serengeti migration. Finally, we insert migratory systems and migration collapse into the broader framework of trophic cascades and explore the implications of migration for community stability, ending with an historic example of migration collapse and its ramifications.

#### 9.1.1 Migration as a special case of movement

A considerable body of work has developed over the last decade on the effects of mobility on food web interactions and ecosystem function (Polis *et al.* 1997; Lundberg and Moberg 2003; Holt 2004; Vanni *et al.* 2004). One intellectual foundation for these studies stems back to the 1970s and the formulation

of the metapopulation concept: discrete populations linked by dispersal, permitting, for instance, regional persistence in ephemeral or disturbance-prone habitats (Levins and Culver 1971; Hanski 1998). Recently, metapopulation biology has been extended to the study of 'metacommunities' i.e., spatial ensembles of communities linked by mobile consumers and seed dispersers at multiple levels (Holyoak *et al.* 2005), and meta-ecosystems, where material and energy flows across space impact local ecosystems (Loreau *et al.* 2005; Varpe *et al.* 2005). These spatial linkages can be expressed by spatial subsidies—the asymmetric transport by organisms or physical transport processes of nutrients and energy across ecosystem boundaries (Polis *et al.*

1997; Anderson and Polis 1999; Stapp and Polis 2003), but also by the cross-ecosystem export of ecological processes; organisms moving from a source ecosystem to a sink ecosystem bring with them changes in levels of predation, competition and mutualism (Holt 2004; Knight *et al.* 2005; Van Bael *et al.* 2008), as well as diseases and new genetic material that change the dynamics of systems compared with what would be expected in closed systems (Lundberg and Moberg 2003).

Despite the fact that much recent research and discussion has been devoted to spatial linkages by organisms between habitats, ecosystems and patches, little work has been devoted specifically to the role of migration as commonly defined. Migration is a special case of movement (Chapters 7 and 8), and we understand migration here not as one-way movement (whether continuous or episodic), but rather as a regular, seasonal pattern of movement that is strongly directional and seasonally reversible (Sinclair 1983; Berger 2004; Mueller and Fagan 2008). Under this definition, we can identify the features of migration, which allow us to disassociate the effects of migratory versus resident animal species on communities and ecosystems (Table 9.1). The aspects of migratory movement that allow us to consider it separately from other forms of movement are:

*Spatial scale.* Although there is a large amount of variation in migration distance both within and between taxa (Berger 2004), migratory movements often occur over larger distances than other forms of movement within the same species (e.g., natal dispersal or foraging within a specific home range; Mueller and Fagan 2008). Studies of cross-ecosystem effects (including nutrient subsidies) often deal

with movements occurring over small spatial scales (Augustine *et al.* 2003), such as the water–land interface (Knight *et al.* 2005) and thus these movements may have qualitatively different effects in terms of their role as vectors (of disease, seeds, or pollen from genetically-distinct populations, for example) to those of animals moving over large distances.

*Timing.* Studies of the impact of mobility across ecosystems are often concerned with movement in response to short-term temporal variation, for example diurnal shifts in feeding patterns between habitats (Augustine 2003; Seagle 2003). Migration usually entails phenological differences with respect to other types of movement, in that it is a highly seasonal process, and this timing effect can be of critical importance (Thrush *et al.* 1994; Takimoto *et al.* 2002; Van Bael *et al.* 2008). For example, animals exposed to seasonal changes in the magnitude of interspecific competition or predation pressure are bound to respond differently depending on whether these competitive pressures occur during times of stress and intraspecific density dependence or not (Van Bael *et al.* 2008). Seasonal predation from a migratory species might have strong negative synergistic effects if combined with food scarcity, for example. For African ungulates, animals that share a wet season range (when food is abundant) with migrants are less likely to be stressed by competitive interactions than are species that share a dry season range (when food is limited; Sinclair 1985). In contrast, disease transmission rates in these systems can be higher in the wet than the dry season. The pastoralist Maasai, for example, avoid mingling their cattle with migratory wildebeest in the Serengeti during the rainy season to minimize the risk of transmission of malignant catarrhal fever from wildebeest to their livestock (Cleaveland *et al.* 2008).

In addition to (and as a result of) being a seasonal process, the timing of migration is highly predictable. This predictability represents a forcing function that may be exploited by resident organisms (e.g., predators) at one end of the migratory range. For example, Serengeti lions (*Panthera leo*) time their reproduction to coincide with the presence of migrant wildebeest. Consequently lions in the dry season range of the wildebeest reproduce roughly

**Table 9.1** Key aspects of migratory systems that set them apart from systems with non-migratory modes of animal movement, and that have important implications for the effects of migration and migration collapse on communities and ecosystems

Property	Migratory system	Non-migratory system
Spatial scale	Large	Small
Timing	Seasonal/Predictable	Seasonal or aseasonal/ unpredictable
Population size	Larger	Smaller

six months out of phase with those in the wet season range.

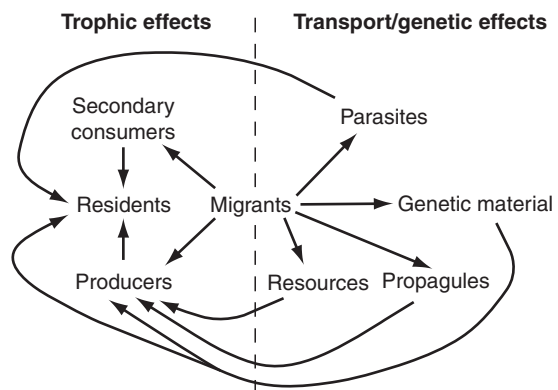
**Population size.** In closed systems, models suggest that seasonal variation in the environment can either depress or increase average population size, depending in a model-specific way on which parameter is fluctuating over time (Holt 2008). But large-scale seasonal variation often tends to depress population size. For instance, if birth rates can be expressed as a saturating function of resource levels then, by Jensen's inequality, temporal variation in resource availability depresses time-averaged birth rates, which in turn tends to depress population size. Migratory species, by avoiding seasons of resource scarcity or heightened mortality risk, may be able to sustain much larger populations than otherwise similar resident species. Indeed, migrants are often far more abundant than their closest resident relatives (Fryxell *et al.* 1988), and their community and ecosystem impacts are therefore bound to be of greater magnitude. Although migration entails costs (e.g., energetic costs, Chapter 5, and a heightened risk of predation or injury), animals that evolve a migratory strategy from a resident one also benefit from more effective exploitation of resources (and therefore escape seasonal limitations in resource availability; Chapter 7) and/or escape from predation and disease (Fryxell and Sinclair 1988b; Bolger *et al.* 2008). Fryxell and Sinclair (1988a), for example, used a mathematical model to show that migratory ungulates in the Serengeti are able to escape top-down regulation by predators, whereas resident ungulates are kept at low population density by predation, a prediction later confirmed by observation (Sinclair *et al.* 2003). A corollary of this is that when ungulate migrations are blocked, this often results in population collapse because the migrant is not adapted to year-round residence in a habitat that is seasonally unsuitable (Bolger *et al.* 2008; Harris *et al.* 2009). The insectivorous parulid warblers that numerically dominate the northern hardwood and boreal forests of North America might face a similar fate if prevented from migrating. These birds can have large impacts upon folivorous insects (Sillert and Holmes 2002), and removing their predation pressure could lead to an upsurge in insect outbreaks, altering forest ecosystem dynamics in a major way. Because species that

undergo mass migrations often become superabundant and play a keystone role in ecosystems, their emergence or disappearance may be of far greater consequence than the emergence or disappearance of similar resident species.

## 9.2 Impacts of migrants on community dynamics and ecosystem processes

### 9.2.1 Trophic versus transport effects

The effects of migrants on communities and ecosystems can be broadly divided into two categories; 'trophic' effects and 'transport' or vector effects (Fig. 9.2). Trophic effects are the result of the direct effects of migrants as providers of a pulse of consumers, competitors, and/or prey. In contrast, transport effects are indirect, and are the result of migratory animals acting as vectors for disease, nutrients and energy, and other materials such as seeds across habitat or ecosystem boundaries. Both of these have potential consequences for both local community and ecosystem dynamics. In a recent paper on the role of animal movement in ecosystem function, Lundberg and Moberg (2003) classified animals as resource,



**Figure 9.2** Potential effects of a hypothetical migratory species on its resident equivalent. We divide effects into two categories: (i) 'trophic' effects, such as competition for a shared resource or apparent competition through effects of the migrant on the population of a shared predator; (ii) 'transport' or genetic effects, in which long-distance movement of resources, genetic material (of the migrant itself or another organism, e.g., pollen) or propagules (e.g. seeds) can affect the resident producer community and productivity and transport of parasites not locally present can affect the population of resident consumers. In this example we assume that the migrant/resident pair are primary consumers, but comparable effects could be extended to migration at a higher trophic level.

genetic or process linkers. Here we take a somewhat broader view and integrate genetic linkages into the transport category (seeds and pollen moved by animals represent the transport of genetic material).

## 9.2.2 Effects of migration on communities

### 9.2.2.1 Competition and facilitation

Migration can impact communities in multi-faceted ways. Even without considering species interactions, many local communities are enriched by migratory species, which persist by utilizing transient pulses of resources, or simply visit en route between their breeding and non-breeding habitats. The outcome of local competitive interactions between species may differ from standard theoretical predictions when one of the species involved is migratory. If a resident species that is a competitive dominant experiences reduced abundance because of seasonal variation, this should free up resources in more benign periods, which could be exploited by a migratory competitive subordinate (Chapter 3). If the migrant is itself competitively superior, its impact on the local community may depend upon the details of its migratory pattern. The competitive pressures imposed by migrants are by definition only present for part of the annual cycle (the seasonality condition above), and the intensity of competition may therefore depend on whether the period of resident/migrant co-occurrence coincides with periods of resource abundance or periods of scarcity (and thus, probable stronger density dependence). In the case of migratory neotropical warblers, for example, some species (black-and-white warblers and American redstarts) are regulated by resources in the wintering range, whereas others (the ovenbird) are regulated by resource availability in the breeding range (Dugger *et al.* 2004). These differences have the potential to affect resident (and other migratory) species in tropical and temperate ranges differentially (competition in wintering areas may have a short-term impact on fitness on adult survival, whereas competition in the breeding range may have a higher long-term impact on fitness by affecting reproductive success).

In the case of the Serengeti, migratory grazers that occupy the south-eastern plains during the

wet season move into the central and northern woodlands during the dry season, when food is scarce (Pennycuik 1975; Sinclair 1979; Sinclair *et al.* 1985; Mduma *et al.* 1999). Resident species that occupy the plains portion of the ecosystem year-round interact (and perhaps compete) with the migrating herds only during periods of food abundance; the opposite is true for grazers that reside year-round in the woodland habitat. Competitive displacement thus might be more conspicuous in the latter habitat.

We can examine this competitive interaction with a theoretical example. We first modified an existing model (the Savanna Dynamics, SD, model; Holdo *et al.* 2009a) of grass (both green and dry), fire, and wildebeest dynamics by introducing buffalo as a typical resident herbivore. We estimated the necessary model parameters to model forage consumption and population dynamics for this species from published data (Sinclair 1977). The SD model partitions the greater Serengeti ecosystem into a spatially realistic grid with a spatial resolution of 10 km. Grass growth and decay and herbivore movement and population dynamics are ultimately driven by rainfall, which we model as monthly surfaces generated from rain gauge data. We draw rainfall years at random from the historical record and thus treat rainfall as a stochastic process, embedded in a strong seasonal forcing function. Wildebeest move weekly across the landscape and their movements and local population growth are determined by green forage intake and the protein content of green forage, which varies spatially and is highest in the plains (Holdo *et al.* 2009b). Buffalo, by contrast, do not move between cells and so are residents at the spatial scale of this model; their population growth rates are based on a negative exponential function (with density-independent birth rates) that relates per capita mortality to per capita total forage intake (both green and dry grass). Owing to their larger body mass, buffalo have a higher tolerance to low-quality forage (dry grass in this case) than wildebeest.

For our present purposes, we ran model simulations for 200-year periods under two scenarios: the default, in which wildebeest are fully migratory, and a 'switched off' scenario, in which wildebeest are initially distributed evenly throughout the

ecosystem and prevented from moving between cells. We examined the simulated response of both the wildebeest themselves and the buffalo. In the default scenario, our model predicted that after about 50 years, the wildebeest and buffalo populations would asymptote at about 1.5 and 0.18 million animals, respectively (Fig. 9.3(a)). Switching off the migration is expected to affect both species. When prevented from efficiently exploiting the entire landscape, the wildebeest population in the model drops dramatically, to about 0.5 million, or roughly a third of its migratory population size (Fig. 9.3(a)). This occurs because the animals resident in the plains are exposed to an almost complete lack of food during the dry season, and woodland residents fail to benefit from the intake of protein-rich grasses in the plains during the wet season. As a result of this decline in the wildebeest population, the buffalo are predicted to increase to a stable population of about 0.2 million when the migration is switched off, due to decreased competition (Fig. 9.3(a)).

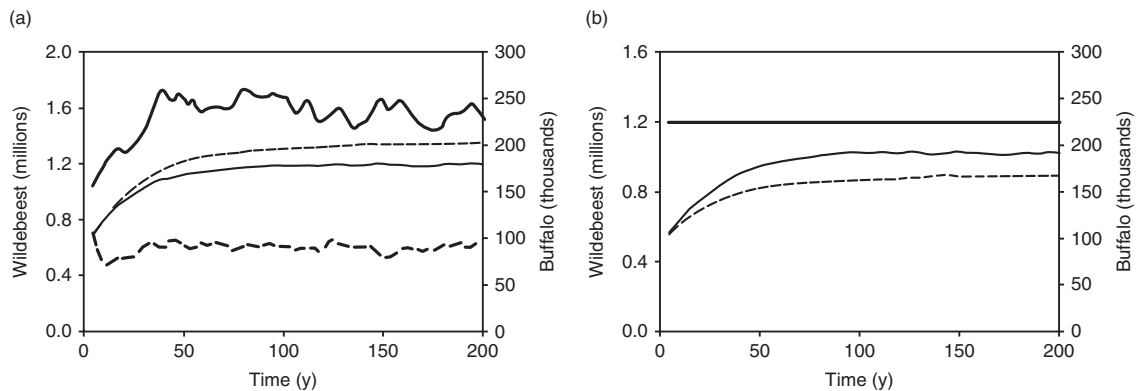
To control for the effect of switching off the migration on the wildebeest, we also repeated the simulations, but fixed the wildebeest at their initial population size of 1.2 million, and distributed uniformly across space. Here the effect on buffalo was reversed; when wildebeest occupy the woodlands year-round, competition for green grass with buffalo is higher during the wet season than would be

the case with a migration, and the buffalo are predicted to stabilize at a lower population than would be the case in the presence of a migration (Fig. 9.3(b)). Given that the wildebeest are present, it would appear that migration itself provides a kind of periodic competitive refuge for the buffalo (although one that is not absolutely required for persistence).

Our simulations show theoretically how the seasonal pulse of competition resulting from migration and the effect of a migratory strategy on the size of migrant populations can affect resident competitors. The effect on the buffalo population is not large because dietary overlap (the ratio of green to dry grass, which can alternatively be thought of as low-fibre and high-fibre components, respectively) is incomplete between the two species (Sinclair 1977). We might expect stronger effects on species that are more similar in terms of diet and body size to wildebeest, such as the resident topi (Murray and Illius 2000).

#### 9.2.2.2 Predation

In addition to affecting resource-mediated interactions between resident and migratory consumers, migration has the potential to exert top-down effects on communities of resident species via its effects on predation pressure, and we have not considered this effect in our example. For instance, year-round residence of wildebeest in the woodlands might



**Figure 9.3** Simulated effect of migration by wildebeest (thick lines) on the resident buffalo population (thin lines) of the Serengeti woodlands. We simulated two scenarios: migration switched on (solid lines) and no migration (dashed lines). In (a) we allowed the wildebeest population to respond dynamically to their food resources, and in (b) we assumed a fixed wildebeest population of 1.2 million. The results shown are based on 5-year moving averages (based on means for 20 runs) of 200-year simulations with stochastic rainfall. We assume no hunting in the system.

potentially offset the negative effect of competition for forage on resident species by diluting their risk of predation (Fryxell 1995). On the other hand, because escape from predation and/or more efficient exploitation of food resources enable migrants to become more abundant than their resident equivalents (Fryxell *et al.* 1988), they may subsidise predators in the resident range, allowing them to become more abundant than would otherwise be the case (Packer *et al.* 2005). This subsidy effect could result in increased predation risk for non-migratory species when the migrants are not present, since the former may go from being 'alternative prey' when migrants are present to becoming a preferred food resource when migrants are absent, with important consequences for their population dynamics (Fryxell *et al.* 1988; Fryxell 1995; Sinclair *et al.* 2003). The population explosion experienced by the Serengeti wildebeest following rinderpest eradication in the 1960s may have had this effect. The abundant wildebeest provided a seasonally-predictable subsidy for lions and hyenas in the Serengeti woodlands (Packer *et al.* 2005), and this may have contributed to the near complete disappearance of the very rare and non-migratory roan antelope (*Hippotragus equinus*) since 1980. Cross-boundary subsidies of predators have been documented in other systems, for example across aquatic-terrestrial interfaces (Sabo and Power 2002). These subsidies can also be experienced at great distances. Densities of insectivorous migratory birds in transit can locally spike to high levels, which could inflict substantial mortality on insect populations.

Multi-trophic interactions modulated by migration are also evident in avian communities in savanna ecosystems. In the Serengeti there are 90 species of Palaearctic migrants comprising 70 insectivores and 20 vertebrate feeders (there are no graminivorous migrants from Asia). In contrast, there are 217 resident insectivores and 61 vertebrate feeders. Systematic transect counts of these resident species over the period 1997–2008 during the season when no migrants were present (May–June) recorded 17 748 insectivores and 448 raptors. The same number of transects when migrants were present (Dec–Jan) provided a similar number of resident insectivores (15 079) and raptors (531), and an additional 3697 Palaearctic insectivores and 268

raptors. Thus, there was an increase of some 20% in insectivore numbers and 60% in raptor numbers (A.R.E. Sinclair, unpublished data). Migrants arrive from the north starting in late August and mostly in September. They follow the monsoonal convergence, the Intertropical Convergence Zone (ITCZ), that moves south in August–December bringing rain storms. These storms are followed by migrating insects, and it is these that are used by the migrating insectivores (Sinclair 1978). In summary, the savanna system, already extremely diverse with resident birds, can only support the large influx of migrants when there is a surplus of food during the rains.

#### 9.2.2.3 Disease

A third mechanism through which migratory species might affect communities is by acting as long-distance disease vectors (Morgan *et al.* 2006; Gilbert *et al.* 2008; Koehler *et al.* 2008). Migrants may act as conduits for long-distance transmission of pathogens that may otherwise have remained spatially restricted. In addition, the seasonal influx of migrants and their resultant mixing with either conspecific or heterospecific residents has the potential to exert a forcing seasonal dynamic on rates of infection in local populations, much as seasonal patterns of school attendance affect the dynamics of flu cases in humans. The basic reproductive number of a disease ( $R_0$ ) is strongly dependent on the pool of susceptible individuals in a population. When a disease is endemic, spikes in infection may occur during periods of migrant influx. The steady-state population size of local populations under these conditions may differ from that expected in the absence of the migratory forcing function. At the same time, the effects of disease (e.g., morbidity or a decline in the ability to mate or disperse) could potentially be dependent on the interaction between dietary stress and the timing of disease. As an example, when rinderpest was enzootic in the Serengeti in the 1950s and 1960s, susceptible calves became exposed to it through contact with livestock during the northern phase of the migration (Talbot and Talbot 1963). This occurred during the dry season, during the time of highest food stress. Talbot and Talbot (1963) speculated that the confluence of dietary stress and infection exerted a synergistic effect, leading to

mortality rates that increased markedly during particularly dry years.

### 9.2.3 Effects of migration on ecosystem processes

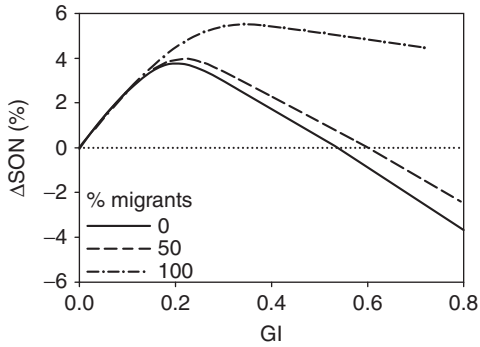
Migratory animals can impact a number of ecosystem processes, such as nutrient cycles and primary productivity, via both direct and indirect pathways. The topic of spatial subsidies, in particular the transport of nutrients and energy across ecosystem boundaries, has received a lot of attention over the last decade (Jonsson and Jonsson 2003; Vanni *et al.* 2004; Varpe *et al.* 2005). Significant downstream effects on nitrogen (N) turnover and productivity in sink ecosystems have been demonstrated as a result of nutrient inputs from source ecosystems by a wide taxonomic range of animal vectors, including fish (Helfield and Naiman 2001; Varpe *et al.* 2005), birds (Post *et al.* 1998), and mammals (Frank *et al.* 1994; Schoenecker *et al.* 2004). These subsidies entail movement, though not always migration. Examples of migratory systems that generate ecosystem-level effects through nutrient transport include anadromous fish (Christie and Reimchen 2005; Varpe *et al.* 2005), geese (Walker *et al.* 2003) and elk (Schoenecker *et al.* 2004). Pacific salmon returning to their natal streams to spawn incorporate large amounts of marine-derived N into riparian habitats, with important consequences for plant primary productivity (Helfield and Naiman 2001).

Less attention has been paid to other effects of animal mobility (especially migration), on ecosystem function. Migrating animals, for example, exert strong effects on their food resources through consumption (Bedard *et al.* 1986; Sinclair *et al.* 2007; Van Bael *et al.* 2008). These direct consumption effects can impact N turnover in ways that differ from the effects of residents (Schoenecker *et al.* 2004; Holdo *et al.* 2007). Holdo *et al.* (2007), for example, combined a two-compartment (plains and woodlands) model of soil N dynamics with functions describing N assimilation, turnover and loss due to herbivory to simulate changes in soil N content and above-ground net primary productivity (ANPP) in the Serengeti woodlands as a function of grazing, migration and fire. The model was based on a series of differential equations describing the dynamics of N

pools (soil organic and inorganic pools, and plant and animal compartments) in the ecosystem (see Holdo *et al.* (2007) for model equations and details). Herbivores can affect the N dynamics of woodland grasses indirectly by transporting N from the Serengeti plains to the woodlands (a spatial subsidy between plains and woodlands), and directly by consuming vegetation. Grazers affect the N cycle by increasing N turnover; N in dung and urine is more readily mineralizable and made available for plant uptake than N in litter (Seagle *et al.* 1992; Ruess and Seagle 1994; Holdo 2007). Simulations also suggested that the timing of grazing is important; resident grazers promote N cycling and enhanced productivity at low and intermediate levels of grazing intensity (because N is limiting), but at high levels of grazing, plant standing biomass is kept low and growth is limited by herbivory (Holdo *et al.* 2007). Excess N is leached out of the system, depressing long-term N availability and ANPP. When the herbivores are migratory, however, they are absent from the woodlands during the growing season, and they therefore do not depress growth during times of maximum productivity (as residents do). This decoupling of the growing and grazing seasons results in a monotonic relationship between herbivore population density and ANPP and soil N in a migratory system, as opposed to a hump-shaped relationship for residents (Holdo *et al.* 2007).

Here we expand on the analysis of resident versus migrant effects in this model to examine how simulated changes in soil organic N in the Serengeti woodlands vary as a function of grazing intensity (GI, the ratio of consumption to ANPP) with different proportions of resident and migratory herbivores (0, 50% and 100% migratory). Our results (Fig. 9.4) suggest that in the absence of fire, the proportion of migrants strongly influences long-term soil N dynamics. Compared with the case with no herbivory, grazing increases soil N up to an optimum level of GI (about 0.2 in our model). When all the grazers are resident, values of GI greater than about 0.55 result in declines in soil N. Increasing the proportion of migrants appears to have a non-linear effect on this threshold; when all herbivores are migrants, even high levels of GI lead to N increases, but this positive effect begins to decline marginally at high grazing intensity (Fig. 9.4).





**Figure 9.4** Simulated effect of grazing intensity (GI, the proportion of total biomass production consumed) on changes in long-term (100-year) soil organic N (SON) content in the Serengeti (against a baseline of no herbivory), as a function of the proportion of migrants versus residents in the herbivore community. We assume no fire in the system.

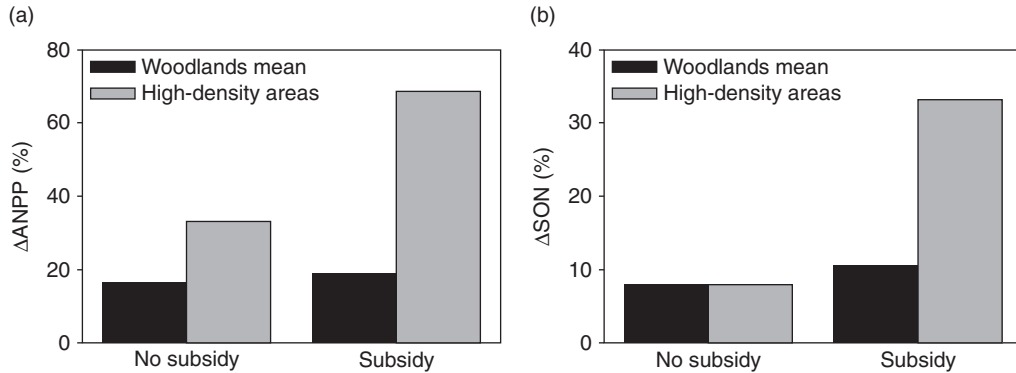
A second effect of migrants derives from their inputs of nutrients. When growth (both in terms of body mass increases and population growth) occurs predominantly at one extreme of the migratory range, and mortality and mass loss are higher at the opposite extreme, a net flow of energy and nutrients occurs between the two seasonal habitats. In the Serengeti, wildebeest increase their body mass and calve in the resource-rich plains, and lose mass and have higher mortality in the woodlands. Holdo *et al.* (2007) simulated the effect of grazing with and without spatial subsidies, in the latter case by assuming no seasonal variation in herbivore N budgets. Over the entire woodland habitat, this subsidy effect is insufficient to have an appreciable effect on soil N budgets and ANPP. The distribution of wildebeest across the landscape is highly heterogeneous, however. Based on monthly survey data, we estimate that close to 10% of the total wildebeest population occupies an area of only 200 km<sup>2</sup> during the dry season, resulting in a local population density (averaged across five months of the dry season) about four times higher than the woodland mean. We modified the simulations in Holdo *et al.* (2007) to compare the average magnitude of the subsidy effect (and the effects of migrants versus residents) with its impact in high-density areas (Fig. 9.5). Our results indicate that, in high-aggregation areas during the dry season, spatial subsidy effects can approximately double the effect of herbivory (versus a baseline of no herbivory) on ANPP and quadruple the effect on soil

organic N. Our estimates show that, at the whole-ecosystem level, the migration results in a net transfer of 0.13 g m<sup>-2</sup> y<sup>-1</sup> of N from plains to woodlands, but local influxes can be as high as 0.5 g m<sup>-2</sup> y<sup>-1</sup>, or about half the combined input of fixation and atmospheric deposition in this ecosystem (Holdo *et al.* 2007). We conclude that the transport of N resulting from migration can therefore be locally important and contribute to enhanced habitat heterogeneity.

#### 9.2.4 Trophic cascades and other downstream effects of migration in ecosystems

In addition to impacting nutrient regimes and regulating their resources, migratory animals can have knock-on effects in ecosystems through cascading effects at multiple trophic levels. Again, the Serengeti migration provides a compelling example of this, as we show that migration collapse in the wildebeest population can lead to coupled changes in grass biomass, fire frequency, and tree cover.

Both empirical (Sinclair *et al.* 2007; Holdo *et al.* 2009c) and theoretical (Holdo *et al.* 2009a) studies have established that wildebeest population size is a key driver of fire frequency in the Serengeti. These effects are mediated by the effect of wildebeest grazing on grass biomass, the main variable limiting the spread of fire across the landscape. Fire, in turn, is the dominant factor driving changes in tree cover (Sinclair *et al.* 2007, Holdo *et al.* 2009a, Holdo *et al.* submitted). We used the SD model to simulate the consequences of migration collapse on ecosystem-wide changes in fire frequency and tree cover. For simplicity, we assumed no elephants and no hunting in the system. As in the earlier example, we conducted 200-year simulations with an initial wildebeest population of 1.2 million animals. The animals were evenly distributed throughout the ecosystem; although it may appear unrealistic not to initially ‘confine’ the wildebeest to either their wet or dry season ranges, this allows us to isolate the effects of lack of movement from area effects, by effectively providing the population with the same total area in both scenarios. In one scenario, we allowed the wildebeest to move weekly throughout the landscape, and in the other scenario we switched off movement to simulate a collapse of the migration.



**Figure 9.5** Simulated effect (with and without a spatial subsidy component) of migratory ungulates on changes in (a) long-term (100-year) net aboveground primary productivity (ANPP) and (b) long-term soil organic N (SON) in the Serengeti, against a baseline of no herbivory. We assume present-day (1.2 million animals) population sizes, and decompose the effects into total effects (grazing effects plus spatial subsidy) and grazing effects only (no subsidy). We also contrast the ecosystem-wide impact (woodland mean—black bars) with the areas of highest dry season population density, a 200 km<sup>2</sup> area that hosts ~ 10% of the wildebeest population during the dry season (high-density areas—grey bars). We assume no fire in the system.

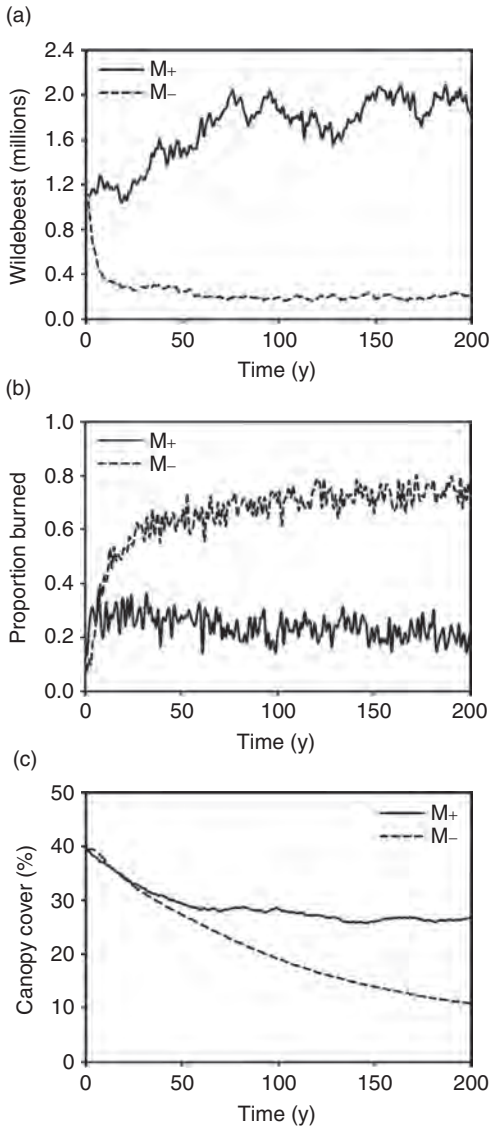
As in the competition example (but now without the buffalo), preventing migration from occurring results in a population collapse in the wildebeest (Fig. 9.6(a)). Note that the collapse is more severe than in the example with buffalo present (Fig. 9.3(a)), because wildebeest–buffalo competition in the SD model is asymmetric (Holdo *et al.* 2009a); whereas wildebeest reduce high-quality food availability for buffalo, buffalo consume some low-quality grasses and thus facilitate enhanced intake of green grass by wildebeest (because green grass in otherwise ungrazed areas is enhanced by reduced self-shading from senescing grasses). The wildebeest collapse is predicted to result in a widespread increase in the area burned each year in the ecosystem (Fig. 9.6(b)). Whereas tree cover is predicted to decline initially under default conditions (although it will stabilize after about 50 years), the decline is more severe and longer-lasting when migration is impeded (Fig. 9.6(c)). This suggests that a migration collapse would have implications not only for the population structure of other herbivores in the grazer guild, but more far-reaching implications for the abiotic environment (fire) and for ecosystem structure.

### 9.2.5 Migration and community stability

There is increasing recognition that spatial processes are fundamental to many ecological processes

(Tilman 1994). Migratory animals, by linking ecosystems, can affect (meta) ecosystem stability (Takimoto *et al.* 2002; Holt 2004) and resilience by acting as sources of ‘external ecological memory’ (Lundberg and Moberg 2003). This topic has yet to be the focus of sustained theoretical and empirical study, but one can imagine that migratory species could exert strong influences on community stability, both to enhance it and to weaken it, depending on the circumstances. Imposing seasonal variation on to multispecies models that in a constant environment tend towards a stable equilibrium can lead to cycles and even chaotic dynamics (King and Schaffer 1999), with overcompensating density dependence leading to low population densities where extinction may be risked. Migratory species may be able to avoid such excursions, and thus reduce their own risk of extinction. Some species can in turn exploit the regularity of these seasonally regular resource pulses. For instance, Eleonora’s Falcon in the Mediterranean has evolved a specialized life history, timing its breeding during the annual cycle to the migratory waves of songbirds each autumn (Del Hoyo *et al.* 1994).

Other resident species may be strongly negatively affected by pulses of consumption, resources, and predation in their local communities, in ways that destabilize communities and ecosystems. A particularly striking example comes from the migratory



**Figure 9.6** Simulated effect of ‘switching off’ the wildebeest migration on (a) wildebeest, (b) fire, and (c) tree cover (in the Serengeti woodlands). We simulated two scenarios: migration switched on (solid lines) and no migration (dashed lines), with an initial wildebeest population of 1.2 million. The results shown are based on means for 20 runs of 200-year simulations with stochastic rainfall. We assume no hunting in the system.

Snow Goose. A combination of reduced hunting and increased food supply on its wintering grounds in Louisiana and Texas, and en route in the Great Plains, has led to an enormous upsurge in its abundance in the Canadian tundra. This in turn has led

to over-exploitation and even collapse of tundra vegetation, which in places has gone completely, leaving behind only extensive mudflats (Jefferies *et al.* 2006).

Conversely, shifts in resident fauna may alter the importance of spatial subsidies and other influences of migratory species. In the Aleutians, the introduction of the red fox decimated migratory seabird colonies, leading to a reduction in nitrogen inputs and a dramatic shift in the plant community from shrub- to grass-dominated taxa. Many pelagic birds nest on sites very far from where they feed in the non-breeding season, and it is likely that introduced mammals on oceanic islands have sharply altered the strength and pattern of nutrient subsidies on island ecosystems.

### 9.3 Collapsed migrations and their consequences: empirical evidence

The models described above predict that the collapse of the Serengeti wildebeest migration would have profound impacts on community structure and ecosystem processes. Indeed it has also been suggested that socio-economic feedback loops including reduced revenues from ecotourism resulting from the loss of the migration, and a subsequent decline in resource protection, could lead to increased illegal hunting and habitat loss and the collapse of the whole Serengeti ecosystem from its present state (Harris *et al.* 2009).

Models can be considered as informed speculation about the consequences of future action. But is there empirical support for the hypothesis that ungulate migration collapse would cascade through ecosystems in the ways that the models suggest? Recent reviews synthesizing the available information on the global status of migratory ungulates have demonstrated that, with very few exceptions (e.g., wildebeest and zebra in Serengeti, white-eared kob (*Kobus kob*) and tiang (*Damaliscus lunatus*) in Southern Sudan and some caribou (*Rangifer tarandus*) populations in Canada and Russia), migratory populations of ungulates are in universal decline and a number of populations have been extirpated (Bolger *et al.* 2008; Harris *et al.* 2009). Is there evidence that migration collapse leads to wider impacts at the community or ecosystem level? We focus here

on ungulate migrations because of the availability of recent reviews and for comparison with the Serengeti models. We also restrict this focus to those ungulates that migrate in large aggregations on the premise that these species are more likely to have a 'keystone' function in ecosystems and thus their removal may have more obvious consequences.

Harris *et al.* (2009) synthesized global data on 23 species of ungulates that historically migrated in aggregations, attempting to describe migration routes, historical and current population size, ecological drivers of migration and conservation threats in a consistent and rigorous manner. The review was challenged by incomplete and outdated information for the majority of migratory ecosystems, with data in most cases being restricted to historical and current estimates of the size of migratory ungulate populations, and little additional information on the wider consequences of migration collapse. With that caveat, we focus on a particular case study where more detailed ecological research has been conducted.

### 9.3.1 Wildebeest in Kruger National Park

The wildebeest migration of Kruger National Park, South Africa, presents an illustrative case study of the consequences of migration collapse. We chose this example because of its similarities with the (still healthy) Serengeti wildebeest migration used to illustrate our theoretical examples above. At proclamation in 1926, Kruger contained low numbers of game as a result of excessive hunting and the 1896 rinderpest epidemic. Early management priorities focused on rebuilding game populations through interventions, particularly the provision of permanent water from boreholes (Gaylard *et al.* 2003). Fencing of the park boundaries for disease control purposes and political boundary demarcation commenced with the southern (1959) and western (1961) boundaries and concluded with the eastern (1976) and northern (1980) fences (Bengis *et al.* 2003). The period 1946–1990 has been described as the era of 'management by intervention', when fencing turned Kruger into a heavily managed ecological island. The consequences of fencing, water provision and management culls of both herbivore and carnivore populations were profound (Freitag-Ronaldson and Foxcroft 2003).

Wildebeest historically migrated between the drier lowveld of southern Kruger and the wetter foothills of the Drakensberg Escarpment, a distance of 100 km (Whyte and Joubert 1988). The size of this population prior to the establishment of the park is unknown but historical accounts indicate that it was heavily impacted by hunting in the late nineteenth century. With the completion of the western boundary fence the migration was prevented and reports suggest that the wildebeest population in Kruger declined by 87% (Whyte & Joubert 1988). The ecosystem effects of the collapse of the migration were, however, confounded by a cascading series of management interventions. Concerns over the declines of wildebeest and zebra populations after the completion of the boundary fence, and modelling, which suggested that predation by lions and spotted hyena was linked to the continued decline (Smuts 1978), led to large management culls of lions and hyena in the 1970s (Mills and Funston 2003). These culls terminated in 1980 when it was discovered that they had no detectable influence on lion density or on population trends of wildebeest and zebra. The provision of artificial water points in the dry northern sector of Kruger had more complex impacts. Following a severe drought in 1982/83, wildebeest and zebra moved northwards from their main range in the central region of Kruger, facilitated by the construction of numerous boreholes and dams in previously waterless areas (Owen-Smith and Ogutu 2003). Lion densities in these areas increased either through immigration or increased reproduction, and lion predation was identified as the key factor causing the decline of the rare roan antelope from 452 in 1986 to 42 in 1993 (Harrington *et al.* 1999). The Kruger case study demonstrates that the ecosystem-level consequences of losing migrations are complex and, in this case at least, interact with multiple other drivers of change, not least anthropogenic factors.

## 9.4 Conclusions and future perspectives

In this chapter, we have attempted to synthesize empirical and theoretical evidence across a range of trophic levels to investigate the broader impacts of migration on ecological communities and ecosystems. Migrations do not occur in isolation; like all

ecological processes, they are embedded in a *milieu* of complex biotic and abiotic interactions and drivers. Migratory species can directly compete with, prey upon, or act as food resources for other species, as well as exerting indirect influences on surrounding animal communities as ecosystem engineers through their effects on nutrient cycles, fire regimes and habitat structure. Much work has been conducted on the role of animal movement for

the transport of energy, materials, genetic information, and disease in ecosystems, but few empirical studies have specifically explored the impact of migration for a wide range of broader ecological processes. Given that habitat loss and fragmentation have led to disruptions or even total collapse of many migrations, there is a pressing need for further empirical work on the downstream effects of migration collapse in real systems.