Ecosystem services provided by arthropods
Schowalter (2000) documents the ways in which arthropods are beneficial in forest ecosystems:
- Maintenance of plant communities via herbivory, disturbance and regulation
- Nutrient cycling via defoliation and decomposition
- Plant propagation via pollination and seed dispersal
- Maintenance of animal communities via disease transmission and predation/parasitism
- Food for insectivorous birds, reptiles and mammals

Arthropods as pollinators and decomposers
Bees, flies, wasps, butterflies, moths, midges, thrips and beetles provide pollination services
Disturbance (fire) opens forest canopy and understory plants flourish along with pollinators
Disturbance may lead to short term disruption of pollinator services in neighboring uncut stands
Collembola and oribatid mites are abundant as decomposers in forest soils ($10^3 – 10^5$ per m$^2$)
Feed on fungi, stimulate mycorrhizae, reduce soil pathogens, and release nutrients
Abundance in litter > organic soil > wood chips, abundance in soil increases with stand age

Insects as disturbance factors
Key insects causing tree mortality in US include defoliators - eastern spruce budworm, western spruce budworm, gypsy moth, and bark beetles - southern pine beetle and mountain pine beetle
Until 1970s insects were considered pests in forest ecosystems, due to short term impacts
Mattson & Addy (1975) introduced to forestry the notion of insects as regulators of forest production, suggesting that outbreaks of defoliators may be beneficial in the longer term

Defoliators as regulators
Insect defoliators directly reduce photosynthetic biomass, but also increase photosynthetic rate per unit biomass via:
- Increased light penetration through canopy
- Reduced competition among trees
- Altered plant species composition in the forest
- Stimulation of redistribution of nutrients within trees (recycling via litter, leaching, frass)
Endemic levels, defoliators consume < 10% of net primary production, but at outbreak levels consumption can be > 100% (multiple years of foliage in conifers)
Simulated defoliation of overstory aspens by forest tent caterpillar (Mattson & Addy)
- longer term impacts of an outbreak (reaching 92% defoliation) are small
- temporary compensation by increased production of photosynthetic biomass
- recovery of stemwood production within 5 years
Simulated defoliation of spruce-fir stands by eastern spruce budworm (Mattson & Addy)
longer term impact is increased stemwood production 20 years after initial defoliation
mature overstory trees most impacted by budworm defoliation
young understory trees released from competition become productive

Predisposition to defoliator outbreaks via foliage quality
Plant tissues have constitutive (continuous) and induced (temporary) defenses
Quantitative defenses (tannins, leaf toughness), qualitative defenses (toxins, monoterpenes)
Plant tissues are of marginal nutritional quality for insects (high cellulose & carbs, low protein)
Defoliator populations respond rapidly to reduced defense or increased nutrition
Low plant vigor (maturity, high stocking density, poor soil, abiotic stress) predisposes forest
stands to outbreaks of defoliators (mostly due to lack of defense?)
Gypsy moth outbreaks (MA) begin on poor ridge top soils, driven by climatic stress

Bark beetles – regulation or disturbance?
Mountain pine beetles selectively attack low vigor, mature trees
Increment cores plot history of attacks in lodgepole pine in attacked (40% mortality) and
unattacked stands, surviving trees in attacked stands show increased stemwood production for 5-20 years after outbreak (Romme et al. 1986)
In western pine-fir forests, outbreaks can influence succession killing pines and releasing firs
Current outbreak in British Columbia has affected 13 million ha (50% mortality), earlier
outbreaks that peaked in early 1980’s showed up to 22% increase in mean basal area of stands
with moderate tree mortality

Defoliators and nitrogen cycling
Defoliation has an immediate effect on nutrient cycles through frass production, insect cadavers,
throughfall, unseasonal leaf litter (all add nutrients to soil) and changes in soil microclimate
Is the burst of nutrient input lost by leaching or immobilized by microbial activity?
Defoliation by oak sawfly (Periclista sp.) in oak, maple, birch forest (NC) in 1998 resulted in:
- greatly increased frass input to soil in May
- greatly increased N input from throughfall in June
- immediate increase in soil nitrates in June/July
- increased export through stream runoff in comparison to non-outbreak years
Experimental additions of either frass or throughfall to soil led to increased abundance of
Collembola and oribatid mites

References
like? Conservation Biology in Practice 2 (Fall): 10-16.
(a) Eastern spruce budworm regulates structure and stemwood production in spruce-fir forest stands in eastern US.

(b) Mountain pine beetles outbreaks kill trees, but can lead to (i) reinvigoration of mature stands of lodgepole pine, or (ii) altered composition of more diverse stands.

(c) Sawfly defoliation impacts nitrogen cycle in North Carolina mixed hardwood forest.

Frass input/Throughfall of nitrate

Soil nitrate/stream export