Insects as pests
Traditionally insects have been considered pests in forest ecosystems.
Key forest pest in US include defoliators - eastern spruce budworm, western spruce budworm, gypsy moth, Douglas-fir tussock moth and tree killers - southern pine beetle and mountain pine beetle.

Insects and ecosystem services
Mattson & Addy (1975) introduced to forestry the notion of insects as regulators of forest production, suggesting that outbreaks may be beneficial in the longer term.
Schowalter (2000) has subsequently documented the various ways in which insects are beneficial in forest ecosystems:
- Maintenance and regulation of plant production
- Nutrient cycling via defoliation and soil decomposition
- Plant propagation via pollination and seed dispersal
- Maintenance of animal communities via disease transmission (vertebrates) and predation/parasitism (invertebrates)
- Food for insectivorous birds, reptiles and mammals

Defoliators as regulators
Insect defoliators directly reduce photosynthetic biomass, but defoliation has indirect effects:
- Increases light penetration through canopy
- Reduces competition among trees
- Alters plant species composition in the forest
- Increases nutrient leaching from foliage
- Increases fall of nutrient-rich litter
- Stimulates redistribution of nutrients within trees
- Stimulates nutrient mineralization in the soil
Endemic levels, defoliators consume < 10% of net primary production, but at outbreak levels consumption can be > 100% (multiple years foliage in conifers)
Leaf chewers and sap suckers - different effects via nutrient recycling?
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 for up to 20 years
- mature overstory trees most impacted by budworm defoliation
- young understory trees released from competition become productive

Insect responses to plant quality
Plant tissues are of marginal nutritional quality for insects (high cellulose & carbs, low protein)
Plant tissues have constitutive (continuous) and induced (temporary) defenses
Quantitative defenses (tannins, leaf toughness), qualitative defenses (toxins, monoterpenes)
Insect performance readily responds to increased nutrition or reduced defense
Low productivity (maturity, high stocking density, poor soil, abiotic stress) predisposes forest stands to outbreaks (mostly due to lack of defense?)
Gypsy moth outbreaks (MA) begin on poor ridge top soils, driven by climatic stress (synchronous across state)

**Bark beetles and forest production**
Endemic mountain pine beetles selectively attack low vigor, mature trees
Outbreaks result in unselective tree mortality as beetles can overcome tree defenses
Differ from defoliators as interaction with decomposition and mineral cycling less obvious
Increment cores plot history of attacks in lodgepole pine in Yellowstone (Romme et al. 1986)
Surviving trees have increased stemwood production for 5-15 years after outbreak
In stands with little understory, outbreaks reinvigorated annual production of surviving trees
In stands with understory, mature trees became less dominant releasing understory and adding complexity to the stand
In western pine-fir forests, outbreaks advance succession killing pines and releasing firs

**Defoliators and nitrogen cycling**
Defoliation can influence nutrient cycles through:
Frass production – rich in nitrogen (> leaf litter), can represent up to 70% of N/P returning to soil
Insect cadavers – easily decomposed, rich in nutrients
Throughfall – nutrient-rich precipitation after defoliation, but may vary with forest type
Leaf litter – altered timing (summer) and quality of foliar fragments
Community composition – different trees alter utilization of nutrients
Root exudates/symbionts – may be affected by defoliation
Soil microclimate – canopy cover and light, temp, moisture
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

**References**
(a) Eastern spruce budworm regulates structure and stemwood production in spruce-fir forest stands in eastern US

(b) Mountain pine beetles outbreaks reinvigorate mature stands of lodgepole pine and alter complexity of more diverse stands

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

Frass input/throughfall

Soil nitrate/stream export