Chapter 16
Insects of Reproductive Structures

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16.1 Introduction

The insects that feed on reproductive structures of forest trees are not only economically important, they are fascinating examples of the ability of insects to adapt to and exploit the many niches available in forest ecosystems. Cones, fruits, seeds, nuts, catkins and pollen are rich food sources available to insect herbivores (Sallabanks and Courtney 1992; Turgeon et al. 1994). These reproductive structures are qualitatively different from vegetative parts of the tree. Their food quality is high relative to leaves, needles, wood and bark (see Sect. 16.3.1.1). Cones, fruits and seeds are discrete packages, often very small and are only present on the tree for a short time. Cone and fruit production are much less predictable through time than other plant structures (Janzen 1971; Crawley 2000). Insects consuming these tissues are forced to adapt to these constraints. In this sense, insects feeding on reproductive structures often behave more like predators than herbivores, searching out and exploiting multiple structures for an individual insect to develop (Janzen 1971; Mattson 1971; Shea 1989). In this chapter we will refer to this group as reproductive structure herbivores.

Fruit, cone and seed feeders have a long evolutionary association with their hosts. As far back as the Late Pennsylvanian Epoch (300 Mya) there is evidence of seed herbivory. The Molteno Formation in South Africa has yielded fossil evidence

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of heteropteran herbivory scars on seeds of several plant genera from the Late Triassic Period (250–200 Mya) (Labandeira 2006). These scars are similar to damage produced by present-day pine seed bugs (Coreidae: *Leptoglossus*) (Krugman and Koerber 1969). Jurassic Period sawflies (Xyelidae) fed on pollen (Labandeira 2006), as do present-day xyelids (Burdick 1961). In contrast, some cone herbivores are geologically recent. Cone beetles (Scolytinae: *Conophthorus*) began diverging from their sister taxon (*Pityophthorus*) in the Early Pliocene (4 Mya). Later glaciation in the Pleistocene may have caused separation of host *Pinus* species ranges which facilitated the evolution of the thirteen extant cone-feeding *Conophthorus* species in North America (Cognato et al. 2005).

Insects attacking conifer reproductive structures are found in the orders Hemiptera, Thysanoptera, Coleoptera, Hymenoptera, Lepidoptera, and Diptera (Hedlin et al. 1981). The Coleoptera, Hymenoptera and Lepidoptera contain the majority of angiosperm fruit and seed consumers (Sallabanks and Courtney 1992). Diversity of genera and species of insects of reproductive structures is notably greater for gymnosperms compared to angiosperms; the more structurally complex conifer seed cones may result in more niche availability (Boivin and Auger-Rozenberg 2016). Species diversity is similar for Western Europe, North America and the Mediterranean Basin (Turgeon et al. 1994; Boivin and Auger-Rozenberg 2016) (see Sect. 16.4.1). Seed losses due to herbivory are often higher in temperate deciduous forests (e.g. 80% loss of acorns due to acorn weevils) than in tropical systems (e.g. 37.8% loss of acacia seeds due to bruchids) (Hulme and Benkman 2002).

Thirteen families feed on cones of conifers in Western Europe; however, only 30 genera have been recorded suggesting specialization for reproductive structure herbivory by a limited number of genera and species (Roques 1991). Specialization also occurs in angiosperms. Larvae of all Bruchidae (Coleoptera) feed and develop primarily within legume seeds, including many leguminous trees and shrubs (Southgate 1979; Derbel et al. 2007).

Insects of reproductive structures typically do not cause unpredictable and catastrophic ecological damage to natural forest stands. Unlike bark beetle and defoliator species, whose eruptive population dynamics can cause major disturbance at the landscape level; cone and seed insects are closely linked to the seasonal phenology of their hosts and their role in forest ecosystems is more subtle, though still important (Turgeon et al. 1994; Boivin and Auger-Rozenberg 2016). Their population dynamics are tied to the periodicity of their host cone or fruit crops (Shea 1989). Generally, fruit and seed herbivory is inversely proportional to crop size (Shea 1989; Turgeon et al. 1994). The larger the seed crop size relative to the size of the herbivore population, the greater the probability that an individual seed escapes herbivory; conversely, the higher the population of seed herbivores relative to the crop size, the more likely an individual seed will be consumed (see Sects. 16.3.3.2, 16.3.4). For example, in white fir, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., smaller crops led to an increase in insect-infested cones (Shea 1989). A bumper crop in natural stands of shortleaf pine, *Pinus echinata* Mill., resulted in a higher proportion of healthy seeds and reduced seed herbivore damage (Mangini et al. 2004). Furthermore, greater insect-caused damage can be expected for the season following a mast year (Boivin and Auger-Rozenberg 2016) (see masting in Sect. 16.3.3.2).

Economically, insects of reproductive structures can limit production of human food and feed products (fruit, nuts, acorns) and impact broader agroforestry services such as carbon sequestration, soil enrichment and biodiversity conservation (Jose 2009). The western conifer seed bug,[1] *Leptoglossus occidentalis* Heidemann, introduced from North America into Italy, is now a serious pest of Italian stone pine, *Pinus pinea* L.; in Tuscany, edible nut collection is no longer profitable because of severe damage caused by this exotic insect (Bracalini et al. 2013; Lesieur et al 2019). Insects destroy holm oak acorns, *Quercus ilex* subsp. *Ballota* (Desf.), in the savanna-like ecosystems of southwestern Spain before they can mature and fall to the ground to be consumed by the endemic Iberian pigs that local farmers use to produce the highly prized hams known as Jamón Ibérico de Ballota (Leiva and Fernández-Alés 2005).

Insects of reproductive structures can have a profound impact on forest ecology because they affect host tree reproduction and demography and can influence the evolution of the host (Boivin and Auger-Rozenberg 2016) (see Sect. 16.3.4). Threatened tree species are particularly susceptible to insects of reproductive structures. The endangered *Juniperus cedrus* Webb and Berthel., endemic to the Canary Islands, suffers seed loss from several seed herbivores (Guido and Roques 1996). Other insects are a major problem in managed trees, primarily in seed orchards and seed collection areas (Coulson and Witter 1984; Turgeon et al. 1994; Boivin and Auger-Rozenberg 2016).

Conifer seed and cone insects were first studied by John M. Miller, Bureau of Entomology, U.S. Department of Agriculture, during 1913–1917 in the western United States (Keen 1958). This work was of little concern until the 1950s when applied tree breeding programs began producing genetically improved seeds for reforestation (Coulson and Witter 1984). Seed orchards were established in Europe and North America to mass-produce genetically superior seed (Zobel and Talbert 1984). Insect damage to cones and seeds quickly became a major factor in the production of costly genetically improved seed (Keen 1958). As a result, seed orchard pest management programs have been developed for many areas and tree species around the world (see Sect. 16.5).

Our objective in this chapter is to introduce the important families, genera and species of insects that feed on reproductive structures by discussing their behavior, ecology and evolution. Our emphasis is a functional description rather than a taxonomic listing of insects of importance; see Ciesla (2011) for a taxonomic treatment. We focus on feeding on reproductive structures prior to propagule dispersal, though post-dispersal herbivory can have important evolutionary consequences (Hulme 1998). We also primarily discuss feeding on female reproductive structures rather than male. The bulk of studies found on this topic are from temperate forests rather

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[1] Insect common names are names approved by either the Canadian Entomological Society or the Entomological Society of America or both.

than tropical, partly because temperate are more heavily studied, and partly because they are used more in sustainable, regenerative forestry than tropical forestry systems.

16.2 Types of Herbivory—Ways that Insects Exploit Reproductive Structures

Various guild classifications have been developed for insect herbivory of tree reproductive structures (Hawkins and MacMahon 1989). Roques (1991) and Turgeon et al. (1994) specified guilds and terminology that accord with the feeding behaviors of conifer-infesting insects. Boivin and Auger-Rozenberg (2016) redefine these guilds to include both angiosperm and gymnosperm herbivores. More focused guilds have been defined for insects feeding on acorns (Fukumoto and Kajimura 2001) and fir cones (Shea 1989). Our approach will be to discuss the modes of feeding on cones, fruits, seeds, pollen and catkins; guilds will become apparent as the types of herbivory are discussed.

16.2.1 Inflorescence Feeders

Many insects are restricted to the consumption of the strobili and conelets of conifers or the buds, catkins, and flowers[2] of angiosperm trees. Others that may infest the inflorescence but complete development after pollination are discussed here.

Some insect species are incidental feeders on inflorescences. Larvae of these species are defoliators by habit but consume reproductive structures when available. Budworms, *Choristoneura* spp. (Lepidoptera: Tortricidae), can defoliate huge areas of spruce and other boreal conifers. In North America, when populations are high, budworms will also feed on strobili and young conifer cones. The eastern spruce budworm, *C. fumiferana* (Clemens) readily consumes buds of balsam fir, eastern hemlock and other species; it can impact cone production for several years during outbreaks (Hedlin et al. 1981). The western spruce budworm, *C. freemani* Razowski (formerly *C. occidentalis* Freeman), will feed on young succulent strobili and conelets of spruce and Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, in the spring before the needles flush.

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[2] Terminology of reproductive structures is that of Bonner and Karrfalt (2008) with modification. An inflorescence is a bud, catkin, flower, or strobilus early in development through pollen release (male) or pollination (female). A strobilus (plural strobili) is the cone-like male or female fruiting body, composed of bracts or scales, of gymnosperms. The female strobilus becomes a cone. A conelet is a young female cone or, for pines, a first-year female cone. A catkin is a dehiscent male flower spike of an angiosperm. The term fruit includes all types (achene, berry, drupe, samara and so on) exclusive of nuts. A nut is a one-seeded fruit with a woody or leathery pericarp (as in *Quercus*), or a fruit partially or wholly encased in an involucre or husk (as in *Carya* and *Corylus*).

Adults can also be incidental feeders. Scarab beetles, *Phyllophaga* spp. (Coleoptera: Scarabaeidae), feed on emerging female strobili in hard pine seed orchards in the southern United States. Feeding beetles damage the female strobili as they enlarge and become receptive to pollen; damaged strobili often die (Ebel et al. 1980).

Other inflorescence herbivores are more intimately tied to the biology of their host species. The looper, *Nemoria arizonica* (Groté) (Lepidoptera: Geometridae), displays larval developmental polymorphism. There are two broods, spring and summer. Larvae of the spring brood feed on oak catkins and their morphology mimics their food, which reduces bird predation. The summer brood larvae develop after the catkins have fallen from the trees. These larvae mimic first-year oak twigs protecting them from avian predation. A randomized diet, temperature, and photoperiod trial demonstrated that the polymorphism is diet-based (Greene 1989).

The small, primitive sawflies in the genus *Xyela* feed on the male strobili of *Pinus* (Ebel et al. 1980). Thirty-two species are known world-wide and fifteen occur in North America (Burdick 1961; Smith 1978, 1979). Adult emergence coincides with the expansion of strobili in the spring. Females oviposit on the expanding strobili. The early instar larvae feed on pollen within the pollen sacs. Mature larvae have been found feeding in the strobili axes of loblolly pine, *Pinus taeda* L. (Mangini unpubl.). Larvae fall to the ground as pollen is shed. They remain as prepupae in the soil and emerge in one or two seasons (Hedlin et al. 1981). Catkin sawflies do not reduce the pollen crop (Hedlin et al. 1981); however, they are nuisances during pollen processing for breeding work, often emerging in huge numbers in pollen drying rooms.

The incidental feeding of budworms and scarabs has little in common with *Xyela* species, whose feeding is tightly coupled with the phenology of their hosts. Inflorescence feeders do not meet the definition of a guild as defined by Root (1967). Inflorescences are the “same class” of resource; but *Xyela* and *Nemoria* exploit them differently than the budworms and scarabs.

16.2.2 Cone or Fruit Feeders

These insects feed internally on the cone or fruit tissues and seeds. These herbivores constitute a major portion of the insects of reproductive structures. Most are obligate internal feeders, having no ability to feed on plant parts other than reproductive structures. They also tend to have higher host specificity than the inflorescence feeder guilds, perhaps as a consequence of their intimate relationship with the substrate. The group can be broken into two categories, coarse internal feeders and determinant internal feeders.

16.2.2.1 Coarse Internal Feeders

These insects indiscriminately consume all internal parts of the developing cone or fruit including the seeds. In most instances this damage is caused by the larval stages; but adults and larvae can both feed during the life cycle of some species. Typically, fruits and cones are infested early in their development; however, some insects attack after cones are nearly mature.

Conifer Insects

Coleoptera. The only Coleoptera in this guild are the cone beetles, *Conophthorus* spp. (Curculionidae: Scolytinae). These are among the most destructive insects infesting pine cones in North America. All but one of the thirteen species infest developing cones; one species, *C. banksianae* McPherson, attacks shoots of jack pine (Coulson and Witter 1984; Ciesla 2011). *Conophthorus* adults are small (2.5–4 mm) dark brown to black beetles. Larvae are C-shaped with brown head capsules. The life histories of species are similar. In late spring, the adult female bores into second-year cones at the base or through the cone stalk. The male follows and after mating, the female makes an egg gallery along the axis of the cone. This girdles the cone and it quickly dies. Eggs laid along the gallery hatch and the larvae feed on the cone tissue and seeds, leaving the cone filled with frass and cone tissue. Brood adults typically overwinter in their host cone (Kinzer et al. 1972; Hedlin et al. 1981). Often, adults will emerge to feed and overwinter in shoots or conelets (Hedlin et al. 1981; Ciesla 2011). The death of the cone is necessary for successful brood development; seed loss is complete even if the larvae do not completely consume the cone. This loss can impact natural regeneration in pine stands (Graber 1964; Kinzer et al. 1972).

Lepidoptera. Coarse internal feeders are well represented by species in the Tortricidae and Pyralidae. Of the Tortricidae, several species of *Eucosma*, known as cone borers, feed in cones and can decrease seed yields in North America (Hedlin et al. 1981; Ciesla 2011). These include *E. cocana* Kearfott on shortleaf pine, *E. rescissoriana* Heinrich on western white pine, and *E. tocullionana* Heinrich, the white pine cone borer, on eastern white pine, *Pinus strobus* L. Life histories vary (Coulson and Witter 1984); however, larvae of all species consume cone contents and leave tightly packed frass and larvae pupate in the ground (Ollieu and Schenk 1966; Hedlin et al. 1981; de Groot 1998). Late-instar *E. tocullionana* often move to fresh cones to complete development. Occasionally, cones are host to both the white pine cone borer and *Conophthrous coniperda* (Schwart), the white pine cone beetle. In Ontario, the beetle, which feeds earlier (mid-May to June) than the borer (mid-June to August), often kills the cone before the borer larvae can enter the cone, giving the beetle a competitive advantage (de Groot 1998).

The coneworm genus *Dioryctria* (Pyralidae: Phycitinae) is by far the most important Lepidoptera that feed on conifer cones and seeds (Hedlin et al. 1981; Whitehouse et al. 2011). Of the 79 species described, perhaps half that number are cone-feeders. They are distributed throughout the Holarctic region; hosts are mainly in the Pinaceae with two species infesting Cupressaceae (Yates 1986; Whitehouse et al. 2011). Adults are small to medium-sized moths with somewhat narrow forewings bearing characteristic crossbands and patches of contrasting colors (Hedlin et al. 1981). Larvae have well-sclerotized head capsules and prothoracic shields, well-developed prolegs and long setae on each segment (Keen 1958; Leidy and Neunzig 1989). Life cycles vary; however, larvae of all species feed internally on the conelets and cones (Hedlin et al. 1981; Coulson and Witter 1984; Whitehouse et al. 2011). Usually, the entire content of the cone is consumed, leaving only coarse frass and webbing within. External evidence of infestation typically manifests as frass and webbing at point of larval entrance. Larvae may infest more than one cone. Depending on host, the dead cones can be distorted or may disintegrate prematurely; the latter, occurring often to pine conelets, can result in inaccurate estimates of damage at cone harvest (DeBarr 1974; Fatzinger et al. 1980).

Some *Dioryctria* are host-specific; others are polyphagous (Roux-Morabito et al. 2008). Pestiferous coneworm species tend to be polyphages, feeding across genera as well as on multiple species in a host genus (Whitehouse et al. 2011). The fir coneworm, *Dioryctria abietivorella* Groté, widely distributed from Alaska to Mexico, throughout Canada and the eastern US, feeds on cones of most Pinaceae in its range (Hedlin et al. 1981; Whitehouse et al. 2011). This insect is a significant pest of white spruce, *Picea glauca* (Moench) Voss, and Douglas-fir seed orchards (Trudel et al. 1999; Roe et al. 2006). Entire cone clusters can be killed and left covered with frass and webbing; larvae even continue to feed in harvested cones stored before seed extraction. The southern pine coneworm, *Dioryctria amatella* (Hulst) infests southern hard pine species in the United States from Texas to Virginia (Coulson and Franklin 1970; Ebel et al. 1980). Larvae can infest strobili, conelets, cones, shoots, rust galls and even wounds in hosts (Hedlin et al. 1981). The life cycle varies by host; in spring overwintering larvae enter shoots of longleaf pine, *Pinus palustris* Miller, or fusiform rust galls on loblolly pine, *Pinus taeda* L. Subsequent generations feed on conelets or cones (Coulson and Franklin 1970). It is a major seed orchard pest in its range (Ebel et al. 1980). *Dioryctria abietella* Denis and Shiffermüeller, the spruce coneworm of Europe, ranges across the Palearctic Region (Knölke 2007) and feeds on species of fir, larch, spruce and pine. It is one of the most important pests of conifer cones in Europe (Roux-Morabito et al. 2008); in Fennoscandia, it is the primary impediment to seed production of Norway spruce, *Picea abies* (L.) Karsten (Rosenberg et al. 2015).

The coarse internal feeders are similar to the white fir "cone and seed mining guild" of Shea (1989) where "Larvae … feed throughout the cone as it develops causing damage to seeds, scales and other cone structures." Larvae of lepidopterans are the major herbivores along with cone beetle adults and larvae in North America. Ecologically, the guild allows us to assess the impact of variable cone crop size on interspecies competition (Shea 1989). For example, the white pine cone beetle, by emerging earlier and killing the cone, prevents the white pine cone borer from attacking the cone (de Groot 1998).

Hardwood Insects

Coleoptera. The acorn and nut weevils, *Curculio* spp. (Curculionidae: Curculioninae), are distributed throughout the world (Hughes and Vogler 2004); most species feed on oak acorns (Drooz 1985); but some consume nuts of hickory, chestnut and birch trees (Williams 1989; Ciesla 2011). Adults possess a long, slender rostrum with tiny mouthparts at the tip; the distinctive snout can be as long as the body or longer (Triplehorn and Johnson 2005). Life histories are much alike for most species. The adult female uses her snout to chew into a developing acorn or nut and then, with her extensile ovipositor, deposits eggs into the nutritious kernel of the nut. The developing larvae feed on the nutmeat, typically consuming it until only frass remains within the husk. Infested acorns often drop prematurely. At maturity, larvae leave the fruit and move to the soil where they remain dormant; pupation and emergence are delayed for one or two years, sometimes up to five years (Drooz 1985).

In North America, several *Curculio* species infest oak acorns. Some, including *C. pardalis* (Chittenden) and *C. proboscideus* Fabricius, have a broad host range; *C. sulcatulus* (Casey) feeds on almost all oak species. In contrast, *C. fulvus* Chittenden is found only on live oak, *Quercus virginiana* Miller (Drooz 1985). Larval feeding can destroy significant portions of nut crops to the detriment of natural oak regeneration and wildlife relying on acorns for food (Gibson 1982). The pecan weevil, *C. caryae* (Horn), feeds on nuts of hickory (*Carya*) species and is a major pest of commercial pecan, *Carya illinoiensis* (Wangenheim) K. Koch, orchards. It causes premature drop of fruits and deformed inedible nuts. The hazelnut weevil, *C. nucum* L. infests hazelnuts in Europe and Asia (AliNiazee 1997). The chestnut weevils of Europe and the Near East, *C. elephas* (Gyllenhal) and *C. propinquus* (Desbr.) feed on acorns and chestnuts. In Mediterranean woodlands, these species cause premature drop of acorns of holm oak and cork oak, *Quercus suber* L. (Cañellas et al. 2007). In France, Italy and the Near East, these two species are key pests of chestnuts, *Castanea sativa* Miller (Paparatti and Speranza 2004). As with their Nearctic counterparts, a portion of the population remain in the soil in extended diapause for one or more years which complicates management efforts (Soula and Menu 2005).

Conotrachelus is a genus of weevils in North America that feeds primarily on oaks and hickories. Three species are common on oaks, *Con.*[3] *carinifer* Casey, *Con. naso* LeConte, and *Con. posticatus* Boheman. Acorns of all oak species are attacked. Life histories are similar to *Curculio*. Adults emerge in late summer, larvae feed inside the nuts, then move to the ground, pupate and remain in pupal cells over the winter. However, *Conotrachelus* species typically cannot penetrate the acorn shell of a sound acorn; oviposition occurs in damaged or previously infested acorns (Gibson 1982). They can attack and oviposit on healthy fruits of hickories (Boucher and Sork 1979).

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[3] In this section, to avoid confusion, we use the following genera abbreviations for repeated scientific names: *C.* for *Curculio*, *Con.* for *Conotrachelus*, and *Cyd.* for *Cydia*.

Lepidoptera. The large Holarctic genus *Cydia* (Tortricidae) contains numerous species of seed and fruit herbivores of economic importance to forestry and horticulture (Ciesla 2011). Many species infest conifer cones (see Sect. 16.2.2.2.1). Several species are coarse internal feeders of *Carya*, *Quercus* and *Fagus* nuts (Drooz 1985; Boivin and Auger-Rozenberg 2016). Native to North America, *C. latiferreana* (Walsingham), the filbertworm, is a key pest of oak acorns and other tree nuts, particularly the European hazel, *Corylus avellana* L., cultivated commercially in the Willamette Valley of Oregon (AliNiazee 1983). Adults are small moths that emerge in June. Females oviposit on leaves near the fruit clusters. Young larvae enter the developing nut at the hilum (where the nut attaches to its husk). They penetrate and feed on the kernel as they develop. Infested nuts drop prematurely, and the mature larvae move into the ground where they overwinter in silken chambers (AliNiazee 1997). Life cycles of other nut-infesting *Cydia* are similar to that of the filbertworm (Debouzie et al. 1996; Speranza 1999; Jimenez-Pino et al. 2011). *Cydia fagiglandana* (Zeller) and *C. splendana* (Hübner) infest chestnuts in commercial orchards throughout Europe and the Near East (Speranza 1999; Brown and Komai 2008). In the Far East, *C. glandicolana* (Danilevsky) feeds on chestnuts in China and is found on acorns in Japan; *C. kurokoi* (Amsel) occurs in China, Korea and Japan and is a common pest of chestnuts in Japan (Brown and Komai 2008). Another European tortricid, *Pammene fasciana* L., called the “early chestnut tortrix”, causes early drop of chestnut fruits; its impact is much less than the *Cydia* species (Speranza 1999; Pedrazzoli et al. 2012).

Coleopteran and lepidopteran secondary pests can make use of the damage created by the primary pests mentioned above. *Blastobasis glandulella* (Riley) (Coleophoridae) is native to the hardwood forests of eastern and central North America. Larvae enter acorns and hickory nuts through holes made by other insects (Drooz 1985) and feed on the remaining contents of the nut, often destroying nuts otherwise capable of germination (Gibson 1971).

In the deciduous forests of eastern North America, *Curculio* spp. and *Cyd. latiferranea* are primary attackers of acorns with *Conotracheles* species and *B. gladulella* acting as secondary scavengers of infested nuts (Gibson 1964, 1971). Other associations of *Curculio* and *Cydia* species occur on oaks in British Columbia and California (Lewis 1992; Rohlfs 1999; Dunning et al. 2002), Europe (Branco et al. 2002; Leiva and Fernández-Alés 2005; Csóka and Hirka 2006) and Asia (Fukumoto and Kajimura 2001; Maeto and Ozaki 2003). In Europe, *C. elephas* and *C. propinquus*, *Cyd. fagiglandana* and *Cyd. splendana*, in various combinations, consume developing hazelnuts and chestnuts (Debouzie et al. 1996; AliNiazee 1997; Speranza 1999) while the guild is represented by several *Curculio* species and *Cyd. gladicolana* in Asia (Fukumoto and Kajimura 2001).

16.2.2.2 Determinant Internal Feeders

The determinant internal feeders follow a definite feeding pattern as they consume the cone or fruit. Typically, this involves the larva of a particular species finding its way into the reproductive structure and then moving to a specific portion of the fruit, usually the seed. Lepidoptera and Diptera are the two dominant orders in terms of the number of species in this category.

Cone Tunnel Makers

Lepidoptera. The genus *Cydia* (Tortricidae) contains several species commonly called seedworms (Hedlin et al. 1981). This genus also includes the filbertworm and other nut consumers (see Sect. 16.2.2.1.2); however, the seedworms have decidedly different hosts and life cycles. Seedworms are found primarily on pine, spruce and fir and are widely distributed across North America and Eurasia (Cibrián-Tovar et al. 1986; Yates 1986; Shin et al. 2018). The adults have a 10–20 mm wingspan; forewings are, with some exceptions, metallic gray with distinct silver crossbands. The creamy white larvae have a shiny brown head capsule. Oviposition behavior of females is synchronized with the host species. Females lay eggs on conelets shortly after pollination in fir and spruce. On pines, with a two-year cone cycle, eggs are deposited in the spring on second-year cones near the cone scale spine (Tripp 1954). The first-instar larva bores into the cone and tunnels between cone scales. It enters the seed and consumes it, leaving it full of frass. The larva repeats this for successive seeds as it develops through 4–5 instars depending on species. The mature larva bores into the cone axis where it overwinters. While overwintering, it tunnels back to a seed and cuts an exit hole then returns to the axis tunnel for pupation. Pupation occurs in spring; the larva forces its way through the exit hole in the seed, pupates in the cone and the moth emerges between opened scales of the cone. Some larvae may diapause for a year (Hedlin et al. 1981).

Seedworms reduce healthy seed yield by directly consuming seeds and can destroy a substantial portion of a seed crop (Hedlin 1967; Bakke 1970). In North America, the important species can be sorted geographically. Species in the southern United States include *C. anaranjada* (Miller), the slash pine seedworm. This unusual species is host-specific to slash pine, *Pinus elliottii* Engelm., and the adults are orange with white crossbands. The pupa has spines on the abdominal segments that help it escape the seed. The longleaf pine seedworm, *C. ingens* (Heinrich) is common on longleaf pine, *P. palustris* Miller, and favors cones on the lower crown. Four seeds per cone are killed per larva, one per instar (Merkel 1963; Coyne 1968). The eastern pine seedworm, *C. toreuta* (Groté), found throughout eastern North America infests southern pines and jack pine, *Pinus banksiana* Lamb., in the Midwest where up to 50% of larvae enter diapause. Moths emerge from extended diapause in large numbers the year after a poor cone crop. Factors that reduce the numbers of first year cones may also increase the percentage of *C. toreuta* larvae undergoing extended diapause (Kraft 1968). In western North America, the ponderosa pine seedworm, *C. piperana* (Kearfott) is a pest of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., and sometimes destroys 50% of the crop. Infested seeds are fused together and to cone scales by silken feeding tunnels (Hedlin 1967). The spruce seed moth, *C. strobilella* (L.), is a significant pest of spruce and is a Holarctic species. In North America, it destroys seeds of all spruce species (Tripp 1954). In Europe, it is a pest of Norway, white and black spruce. A cold period is required for adult emergence (Bakke 1970). There appears to be a difference in the pheromone components between North American and Swedish populations, suggesting that the two populations may be separate species (Wang et al. 2010; Svensson et al. 2012). Several species are pests of conifers in Asia (Shin et al. 2018).

Diptera—Anthomyiidae. Often called cone maggots, species in the Holarctic genus *Strobilomyia* (Brachycera: Anthomyiidae) feed as larvae in the cones of spruce, fir and larch in boreal and montane habitats. Michelsen (1988) erected the new genus *Strobilomyia* for the monophyletic cone- and seed-feeding anthomyiids formerly placed in *Hylemya* or *Lasiomma.* Twenty species have been described; most species are pests of *Larix* with a few found on *Abies*, *Picea* and *Tsuga.* Adults are moderately hairy, small flies that resemble house flies. Arista of antennae are plumose. The larvae are typical brachycerine maggots with visible mouth hooks and tubercles on the posterior. The pupae occur in puparia formed from the last larval cuticles (Hedlin et al. 1981; Triplehorn and Johnson 2005).

Strobilomyia earn their place as determinant internal feeders by the intricate feeding pattern the larva makes as it feeds within a developing cone. Females oviposit on or near the conelet and the first instar remains in the egg. The second and third instars make a spiral feeding tunnel around the cone axis, consuming seeds and cone tissue as they tunnel. Some species, such as *S. laricis* Michelsen, move through the cone axis as they complete their development (Roques et al. 1984; Sachet et al. 2006, 2009). The mature third-instar larva drops to the ground during moist weather, usually in mid-summer. It forms a puparium in the ground litter where it overwinters. The small cones of larch typically host one larva while the larger cones of fir and spruce may have several. There is only one generation per year, consonant with the yearly cone cycle of the host trees (Michelsen 1988). A portion of the population enters extended diapause. In the Alps, prolonged diapause of *S. anthracina* (Czerny) coincided with poor cone crops of Norway spruce, *Picea abies* (L.) Karst. Diapause was initiated prior to onset of winter and may be correlated with a lack of available oviposition sites (Turgeon et al. 1994; Brockerhoff and Kenis 1996) (see Sect. 16.4.4).

Strobilomyia inhibit normal development of cones; larvae are robust feeders and can impact seed production in orchards (Roques et al. 1984; Michelsen 1988; Sweeney and Turgeon et al. 1994). In the western United States, there may be four or five *S. abietis* larvae in a fir cone. Cones with multiple larvae may die in early summer; all their potential seed is lost. Up to 30 percent loss of seed has been recorded. In North American spruce, *S. neanthracina* Michelsen, is a major pest, sometimes destroying entire seed crops (Hedlin et al. 1981). The number of seeds eaten per cone is positively correlated to the size of the cone; this impacts seed orchards where large cones are desired (Fidgen et al. 1998). In France, European larch, *Larix decidua* Mill., hosts *S. laricicola* (Karl) and *S. melania* (Ackland), which together can result in 50–60% damage to cone crops and an impact on natural regeneration in the French Alps (Roques et al. 1984). Other species cause similar damage to *Larix* throughout Eurasia (Michelsen 1988; Roques et al. 1996).

Cone and Fruit Galling Insects

Conifer Galling Insects. A gall is an abnormal, localized growth of plant tissue caused by the parasitic activity of another organism (Redfern and Shirley 2002). Insects and mites induce and inhabit galls; they gain protection from hygrothermic stress and access to enhanced nutritional resources (Price et al. 1987). Although not abundant among insects of reproductive structures, several gall-makers are important pests.

The family Cecidomyiidae (Diptera: Nematocera) is a large family (>6000 species) containing many destructive agricultural pests. It is also the largest gall-making group of arthropods (Gagné and Jaschhof 2014). Strangely, few species seem to be important on conifers. The Douglas-fir cone gall midge, *Contarinia oregonensis* Foote, is found throughout the range of Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, from central British Columbia down through north-central Mexico and throughout the Rocky Mountains. It is perhaps the most significant cone pest of Douglas-fir in the Pacific-Northwest (Hedlin 1961; Hedlin et al. 1981). The adults, typical midges, are fragile and tiny, only 3–4 mm long, with spindly legs. Eggs are about the width of a Douglas-fir pollen grain, but several times longer. The grub-like headless larvae are white in early instars, gradually becoming orange. Pupae are dark orange (Hedlin 1961). Adults emerge in spring when Douglas-fir flowers are open for pollination; emergence is closely tied to host phenology. The female deposits eggs at the base of the opened cone scale. Larvae tunnel into the cone scale and cause a gall to form near the ovules, each larva in a separate cell where it feeds on gall tissue. In autumn, during wet weather, the larva drops to the ground and pupates in a delicate cocoon in the litter, often in a dead male Douglas-fir strobilus. Pupation occurs in early spring. A portion of the population enters diapause for one or more years (Hedlin 1961).

Damage occurs as seeds are fused to the cone scale by the galls formed near the seeds. There are usually multiple galls in a cone scale. When large numbers of larvae are present, the scales die, and all seeds are lost. At times, hundreds of larvae can be found in a single cone. Damage becomes visible in July and August as scales die and turn red (Hedlin et al. 1981).

Hardwood Galling Insects. The cecidomyiids and gall wasps in Cynipidae (Hymenoptera) cause galls in hardwood trees, typically on leaves but also on flowers and fruits. On oak acorns, the cynipid genus *Callirhytis* causes galls on oak acorns. In North America, *C. fructuosa* Weld forms hard, lignified “stone” galls within the acorn. *Callirhytis operator* (Osten Saken) forms a “pip” gall in the side of the acorn shell. The pip gall causes the acorn to drop prematurely while the stone galls destroy the seed contents (Gibson 1982). Eurasian species cause similar galls in acorns (Csóka and Hirka 2006). A full treatment of the vast array of species and habits of hardwood gall feeders is beyond the scope of this work; literature compendia include Melika and Abrahamson (2002), Abe et al. (2007) (Cynipidae) and Gagné and Jaschhof (2014) (Cecidomyiidae).

Cone Scale-Feeding Insects

Midge larvae (Diptera: Cecidomyiidae) are common on or in conifer cone scales and bracts. Species in the genera *Asynapta*, *Camptomyia*, *Cecidomyia*, *Contarinia*, *Dasineura*, *Kaltenbachiola*, and *Resseliella* feed between the cone scales of the developing cone. Most are not serious pests but can impede the normal development of the cone when they induce resin that fuses cone scales together (Hedlin et al. 1981). *Asynapta hopkinsi* Felt is widely distributed in North America on fir, pine and spruce and feeds on resin exuded between cone scales (Hedlin et al. 1981). *Cecidomyia bisetosa* Gagné deforms cones of slash pine in the southern United States (Ebel et al. 1980). The Douglas-fir cone scale midge, *Contarinia washingtonensis* Johnson, occurs in western North America. It resembles *C. oregonensis*; however, it does not cause galls. Eggs are laid beneath cone bracts in early summer. Larvae make longitudinal tunnels under the surface of scales. Larvae drop to the ground and overwinter in cocoons in the litter. It can be abundant but does not cause significant damage (Johnson 1963). Species of *Kaltenbachiola* and *Resseliella* are common in Europe (Skrzypczyńska 1985, 1998).

16.2.3 Seed Feeders

Insects that feed within the seed represent the most specialized of the insects of reproductive structures. The life cycles or morphology of these species allows individuals to breach the developing seedcoats. Once access to the seed has been gained, the insect consumes the inner contents consisting of the embryo and either the megagametophyte (gymnosperms) or the endosperm (angiosperms) (Bonner and Karrfalt 2008). Access to the seed may be external (exophytic) by means of specialized mouthparts or internal (endophytic) by means of a life stage, usually the larva, physically entering the seed. The obligate seed-feeding insects tend to be even more specialized and host-specific than the Cone and Fruit Feeders, again because of their intimate association with the host plant.

16.2.3.1 External (Exophytic) Seed Feeding Insects

The seed-feeding true bugs (Hemiptera: Heteroptera) feed on the nutritious seeds hidden within cones and fruits; yet all life stages occur outside the cone or fruit. Only their piercing-sucking mouthparts invade their hosts. The mouthparts form a bundle of needle-like stylets within a segmented sheath. When feeding, the bug injects saliva through a duct in the stylet. The saliva liquefies the contents of the seed. The bug sucks out the liquid through the stylet. Typically, there is little external evidence of feeding damage (Hedlin et al. 1981). Only a handful of species are involved in each of the families Coreidae, Lygaeidae, Miridae, and Scutelleridae.

Coreidae—Leaf-footed Bugs. This family of medium to large bugs are elongate and usually dark colored. The common name comes from the expanded and leaf-like hind tibiae common to most species. They have scent glands that give off a strong odor when the bugs are disturbed. Most are plant-feeders (Drooz 1985; Triplehorn and Johnson 2005). Two species damage conifer seeds in North America, the leaf-footed pine seed bug, *Leptoglossus corculus* (Say), and the western conifer seed bug, *Leptoglossus occidentalis* Heidemann. Both are similar in appearance and habits. Adults are 15–18 mm long, with a narrow head and prominent eyes. Characteristic narrow white zigzag cross-bands are on the forewings. Nymphs are similar in color to the adults. Eggs are semi-cylindrical (Hedlin et al. 1981). Adults overwinter in sheltered locations, often in buildings.[4] On emerging in spring, they feed on male strobili. Adults are good fliers and make a distinctive buzzing sound when in flight. Females lay eggs on needles throughout the spring and summer. First-instar nymphs do not feed. Second-instar nymphs feed on developing ovules in conelets. Older nymphs and adults feed through the summer on seeds in maturing cones (Hedlin et al. 1981). *Leptoglossus occidentalis* typically has one generation per year; *L. corculus* may have several generations (Hedlin et al. 1981). The bug pushes its mouthparts through the scale to the seed. Saliva softens the seed coat, which is then punctured, and the bug sucks out the contents after the saliva liquefies the tissues. The puncture is marked by a minute hole in the center of a spot of discolored tissue (Koerber 1963).

Leptoglossus occidentalis is native to western North America but has extended its range eastward into the Midwest (McPherson et al. 1990). First reported by Koerber (1963), it is a major seed orchard pest in the Pacific Northwest and Rocky Mountains. It feeds on a wide range of conifers but is of most concern on Douglas-fir and pines, causing extensive seed loss (Bates et al. 2000; Strong 2015). Feeding before the seed coat hardens causes fusion of the seed to the cone scale, feeding after hardening results in an empty seed. Feeding on conelets by second-instar nymphs causes conelet abortion (Krugman and Koerber 1969; Connelly and Schowalter 1991; Bates et al. 2002,). Management of *L. occidentalis* is difficult. Separating natural abortion from bug-caused abortion makes damage assessment difficult (Bates et al. 2000). Damage occurs throughout the season and varies with host phenology (Strong 2006). Bugs are difficult to monitor, prompting studies on their communication (Takács et al. 2008) and host location cues (Takács et al. 2009) in an effort to exploit their behavior for management.

In 1999, *L. occidentalis* was discovered in Italy and has since become a major invasive pest, spreading throughout Europe from Portugal to Turkey (Roversi et al. 2011). It is the exemplary invasive insect. Highly mobile themselves, adults readily hitch rides with humans, and they are physiologically labile, easily adapting to new hosts and habitats (Tamburini et al. 2012). In Italy, *L. occidentalis* has dramatically reduced commercial pine nut production from and reduced regeneration of Italian stone pine, *Pinus pinea* L. (Bracalini et al. 2013; Lesieur et al. 2014). It has been

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[4] On occasion *Leptoglossus* and other true bugs seeking shelter will invade homes in huge numbers causing major annoyance to homeowners. *Leptoglossus occidentalis* adults have even caused home damage by piercing plastic plumbing with their sturdy mouthparts (Bates 2005).

implicated as a potential vector of *Diplodia sapinea* (Fr.) Fuckel, the causal agent of a tip blight in European pines (Luchi et al. 2012).

Leptoglossus corculus, found throughout the eastern and southern United States, attacks most pine species in its range. Similar in appearance to *L. occidentalis*; it can be separated by its dilations on the hind tibiae which extend nearly to the apex, the dilations are much shorter in the latter (Allen 1969). The leaf-footed pine seed bug was long overlooked as a significant pest because its damage was not obvious (DeBarr 1970). It is one of the most destructive insects in southern pine seed orchards (Hedlin et al. 1981). Second-instar nymphs feed on conelet ovules and cause conelet abortion (DeBarr and Ebel 1974; DeBarr and Kormanik 1975). Later-instar nymphs and adults feed on seeds in second-year cones. As with its western counterpart, actual damage is difficult to estimate because seeds damaged before the seed coat hardens are often overlooked (DeBarr and Ebel 1973). In southern pine orchards, *L. corculus* occurs in combination with another seed-feeding bug, *Tetyra bipunctata* (Herrich-Schäffer) (Scutelleridae) (DeBarr 1967).

Scutelleridae – Shield-backed Bugs. The Scutelleridae are similar to stink bugs (Pentatomidae) but distinguished by the scutellum which extends over most of the abdomen like a shield (Triplehorn and Johnson 2005). *Tetyra bipunctata*, the shield-backed pine seed bug, occurs on all pines in the eastern United States. Adults are robust brown to dark brown insects with dark pits on the scutellum and 11–15 mm long. Nymphs are oval, flattened and grey to red-brown in color. Eggs are spherical and green changing to red as they mature. Adults overwinter under duff at the soil surface and emerge in April. Eggs are laid on needles and cones from late July through September. First-instar nymphs do not feed, later-stage nymphs and adults feed on seeds of second-year cones (Hedlin et al. 1981). After oviposition in spring, the adults enter an obligate dormancy—adults do not feed before mid-summer. *Tetyra bipuncata* can occur in large numbers but is not considered a major pest in southern orchards. Its single yearly generation and obligate diapause limit its feeding to mid-summer through fall. In contrast, *L. corculus* feeds from early spring through cone harvest, it has several generations and second-instar nymphs through adults can destroy seeds (DeBarr and Ebel 1973; Cameron 1981).

Lygaeidae. Species in several genera of Lygaeidae feed on cones and fruits. *Belonochilus numenius* (Say), introduced from North America, feeds on the fruiting heads of *Platanus* species in Europe and the Mediterranean Basin (Gessé et al. 2009). Four species of *Orsillus* feed on cones and seeds of Cupressaceae in Europe and can reduce seed yields (Dioli 1991; Rouault et al. 2005). *Orsillus depressus* Mulsant and Rey feeds on native and exotic species of *Juniperus* and *Cedrus* and is common in the Iberian Peninsula (Ciesla 2011). *Orsillus maculatus* (Feiber) is a pest of *Cupressus sempervirens* L. cones (Ciesla 2011) (see Sect. 16.3.1.4). *Orsillus* may be a potential vector of *Seridium cardinale* Sutton and Gibson, the causal agent of cypress bark canker disease (Rouault et al. 2005). The elm seed bug, *Arocatus melanocephalus* Fabricius (Hemiptera: Heteroptera: Lygaeidae) is native to Europe and widely distributed in Central and Southern Europe (Ferracini and Alma 2008); it was reported as an invasive in China in 2013 (Gao et al. 2013) and subsequently in North America (Idaho State Department of Agriculture 2013; Acheampong and Strong 2016).

Miridae. The mirid *Platylygus luridus* (Reuter) feeds on ovules of jack pine conelets and causes their abortion (Rauf et al. 1984). The birch catkin bug *Kleidocerys resedae* feeds on reproductive structures of birch as well as seeds of many other species (Wheeler 1976), but it is not known to cause economic damage.

Rhopalidae. In North America, the boxelder bug, *Boisea trivittata* (Say), and the western boxelder bug, *Boisea rubrolineata* (Barber), feed on ash and maple samaras, primarily on boxelder, *Acer negundo* L. in summer and fall. The boxelder bug occurs in the East and extends west to Montana and Alberta; its western counterpart occurs from British Columbia to Texas. Both species are similar in appearance and habitat and have little impact on host trees but are nuisances when they enter houses for overwintering (Tinker 1952; Ciesla 2011).

16.2.3.2 Internal (Endophytic) Seed Feeding Insects

Internal seed-feeding insects are those which must complete one or more life stages, almost always the larva and pupa, within the seed, consuming the seed contents as they develop (Turgeon et al. 1994). Internal seed feeders are considered the most specialized consumers of reproductive structures (Roques 1991). Species in Coleoptera, Hymenoptera and Diptera are involved.

Hymenoptera. The seed chalcid wasp genus *Megastigmus* (Chalcidoidea: Torymidae) is by far the largest group of conifer internal seed feeders (Grissell 1999). This group contains 41 species of seed insects associated with the Pinaceae, Taxodiaceae and Cupressaceae. Geographically, they seem to be restricted to the Holarctic region (Auger-Rozenberg et al. 2006). These pests are generally highly species-specific, but some can infest several members of the same genus. *Megastigmus* species have one generation per year and are most abundant on conifers with yearly cone cycles; but some species infest *Pinus* (Kinzer et al. 1972; Hedlin et al. 1981; Cibrián-Tovar et al. 1986).

Megastigmus adults are small- to moderate-sized (3–5 mm in length) antlike wasps with elongate, enlarged hind coxae, laterally compressed abdomens, and a long ovipositor in females. The forewing has a large, dilated darkened spot (stigma) in its anterior margin. Adults are variable in color with patterns of black, brown and yellow (Keen 1958; Hedlin et al. 1981). Eggs are spindle-shaped. Larvae are legless and strongly curved or arched, giving a c-shaped appearance. Pupae are exarate. Both larvae and pupae occur within the seeds and can only be seen by dissection or radiography (Hedlin 1956; Skrzypczyńska 1978). Typically, the overwintered adult emerges in spring and early summer from seed that has been shed from the tree. A small circular hole is cut in the seed coat by the emerging adult. After mating, the female lays her eggs directly inside the host ovules by inserting the ovipositor through the scales of the young cones. All the immature stages will then develop inside the seed. Pupation occurs in spring.

Megastigmus, as a group, is a major seed destroyer of conifers. Species consistently cause damage in managed seed orchards throughout the Holarctic. Because of the high level of specialization of these seed parasitoid species and their intimate relation with their hosts, seed chalcids have evolved a series of adaptive traits to cope with the wide spatial and temporal fluctuations of conifer seed production. These adaptations include extended diapause (Suez et al. 2013), parthenogenetic reproduction (Boivin et al. 2014), effective dispersal (Jarry et al. 1997; Lander et al. 2014), and the ability to modify the physiology of seed development in ways similar to galling insects (von Aderkas et al. 2005). The ease of invasive introduction and the peculiarities of the life cycle have made seed chalcids the subject of much genetic and behavioral research (Boivin et al. 2017) (see Sects. 16.3.1.4, 16.3.3.1, 16.4.3, 16.4.4).

The Douglas-fir seed chalcid, *Megastigmus spermotrophus* Wachtl, native to the natural range of Douglas-fir, *Pseudotsuga menziesii*, has been introduced into areas where Douglas-fir is grown commercially including Great Britain, Western Europe and New Zealand (Hussey 1955; Mailleux et al. 2008). In the Pacific Northwest, it is a major seed pest in orchards (Hedlin et al. 1981). *Megastimus albifrons* Walker is one of the rare seed chalcids attacking *Pinus*; hosts are ponderosa pine, *Pinus ponderosa*, and several *Pinus* species in Mexico. It has the typical one-year life cycle. Seeds often remain in cones and the adults must escape the seed and tunnel through the scale to disperse (Kinzer et al. 1972; Cibrián-Tovar et al. 1986). The spruce seed chalcid, *M. atedius* Walker and the fir seed chalcid, *M. pinus* Parfitt attack *Picea* and *Abies* species, respectively, and are native to North America but established in Europe. Numerous species are native to Europe and Asia including *M. pictus* (Förster) on Eurasian species of *Larix* (Roques et al. 1995; Roques and Skrzypczyńska 2003).

Coleoptera. *Lignyodes bischoffi* (Blatchley) and *L. helvola* (LeConte) (Curculionidae) are weevils native to eastern North America. They feed on seeds of *Fraxinus*. Females oviposit on seeds, the larvae consume the seed, and overwinter in the seed or on the ground (Barger and Davidson 1967). *Lignyodes bischoffi* has been introduced into Central Europe (Gosik et al. 2001).

Diptera. Species of *Earomyia* (Brachycera: Lonchaeidae), called seed maggots, are found primarily on *Abies* but also occur in, *Larix*, *Picea*, *Pseudotsuga*, and *Tsuga* (McAlpine 1956). Adults are small shiny black flies with wings longer than the abdomen, which is flattened. The larvae are typical brachycerine maggots. Females oviposit on cone scales in late spring. Newly hatched larvae enter the cone and then penetrate the seeds to feed. In fall, the mature larvae drop to the ground, form puparia, and overwinter. Some may delay emergence for a year or two (Keen 1958). In North America, *Earomyia abietum* McAlpine, *E. brevistylata* McAlpine, and *E. longistylata* McAlpine infest only *Abies*; *E. aquilona* McAlpine infests *Abies*, *Larix* and *Pseudotsuga* and *E. barbara* McAlpine is found on those genera and *Picea* and *Tsuga* (McAlpine 1956). In Europe, *E. impossible* is common on *Abies* (Skrzypczyńska 1998). Seed maggots often occur in large numbers but are not usually significant pests (Hedlin et al. 1981).

Gall midges in the genus *Semudobia* form galls within the developing seeds of birch. Several species attack birch in the palearctic, nearctic, or nolarctic (Roskam

1977). One species also galls the catkin scales. *Semudobia* larvae are the basis of a suite of inquilines, chalcid parasitoids, and predators (Roskam 2013).

16.2.4 Tropical Ecosystem Herbivores of Reproductive Structures

Tropical forests are characterized by rich biodiversity in both host trees and their insects. Masting is important in tropical forest ecosystems (Herrera et al. 1998). For example, in Sarawak, Malaysia, community-wide masting or "general reproduction" occurs at intervals of 2–10 years. At general reproduction, most plant species in the community flower synchronously over a period of three to six months followed by mass dispersal of seeds (Asano et al. 2016). Seed herbivore satiation is the accepted explanation for such masting; the abundance of seed overwhelms herbivore consumption leaving a large seed crop for regeneration while in non-mast years, herbivores are starved (see Sect. 16.3.3.2) (Hosaka et al. 2009; Linhart et al. 2014; Asano et al. 2016).

Tropical tree seed herbivores consist primarily of species of Coleoptera, Lepidoptera, Hemiptera and Hymenoptera. Weevils (Curculionidae, Nanophyidae) and Lepidoptera (Pyralidae, Tortricidae) consume seeds of dipterocarps (Dipterocarpaceae), primary components of rainforests of Southeast Asia (Hosaka et al. 2017; Lyal and Curran 2000). Australian eucalypts (Myrtaceae), sheoak (Casuarinaceae), and tea tree (Myrtaceae) host anobiid beetles and chalcidoid wasps (Andersen and New 1987). Curculionoidea infest seeds of baobab (Malvaceae) and mangrove (Rhizophoraceae). Bruchid beetle larvae infest seeds of Amazonian palms (Arecaeae) (Silvius and Fragoso 2002) and are major consumers of tropical acacia (Fabaceae) seeds (Janzen 1969; Peguero et al. 2014). Bugs (Lygaeidae) feed on seeds of figs (Moraceae) (Slater 1972). Much remains to be learned about tropical seed herbivores (Basset et al. 2019).

16.3 Reproductive Structures as Habitat, and Evolutionary Consequences for the Host

Reproductive structures offer a unique habitat that is both nutrient-rich and well-defended. Herbivores have devised many mechanisms to exploit this resource, while hosts have evolved means to limit herbivory. This section explores these relationships, and places them in an evolutionary context.

16.3.1 *Reproductive Structures Nutritive Value and Host Defenses*

16.3.1.1 Nutritive Value

Most plants invest substantial resources in seed development, quantitatively to compensate for pre- and post-dispersal losses, and qualitatively to provide their embryos with enough reserves to germinate successfully. Consequently, seeds and reproductive structures, in general, are a greater source of carbohydrates and proteins than most other plant parts (Hulme and Benkman 2002) (Fig. 16.1). Seeds are also long lasting, offering long-term storage of nutrients that seed herbivores can exploit. Fruit and other non-seed reproductive structures can also be rich resources, but are more transient, and can be considered similar to dung or carrion (Lukasic and Johnson 2007). Because of lower defenses and increased transience, non-seed reproductive structures often undergo a distinct succession of species utilizing them, much like dung or carrion. Nutrient extraction from seeds can be improved with bacterial symbionts, such as *Burkhoderia* in *Megastigmus*, which aides in nitrogen recycling and nutrient breakdown of the megagametophyte (Paulson et al. 2014).

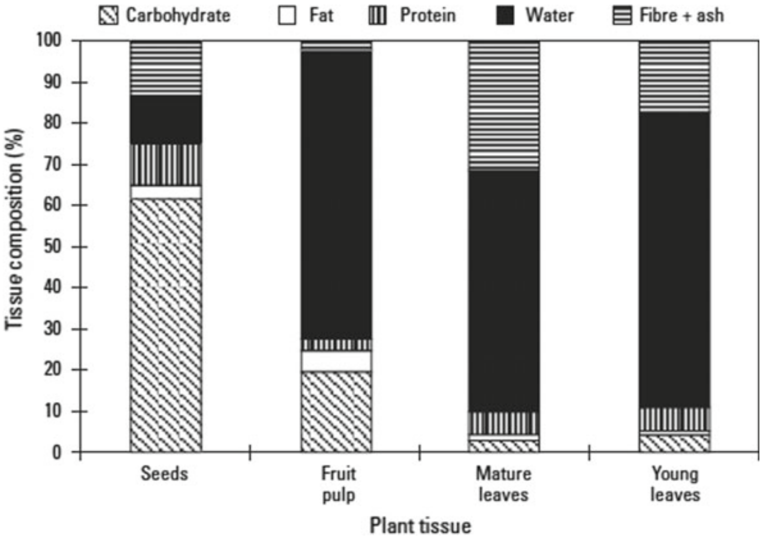

Fig. 16.1 Comparison between the average composition of seeds and other plant parts. Seeds provide a concentrated nutrient source that is particularly rich in carbohydrates. From Hulme and Benkman 2002

16.3.1.2 Chemical Defenses

Plant chemical defense strategies against herbivory are ubiquitous and explain many plant–insect interactions. While a large amount of information has been gathered on chemical defenses of vegetative parts, much less is generally known with regards to reproductive structures. In practice, it has long been established that a wide variety of toxins and repellents occur in seeds. Some tree seeds, such as those of the neem tree, *Azadirachta indica* A. Juss, even provide extracts used as insecticides or insect repellents.

Seed chemical defenses include tannins that interfere with protein absorption, cyanide precursors, enzymes inhibitors and phytohaemaglutinins that disrupt enzyme functions (Bell 1978). Defense compounds are often complex molecules that require significant energy and metabolites to synthesize. As such, their physiological cost is often significant. They also need to be stored in the seeds, thus limiting the space available for reserves destined to the embryo and the seedling. This limitation is sometimes mitigated by synthesizing toxins that can be metabolized and used by the seedling later (Harborne 1993).

Defense chemicals can also be synthesized as an induced response to herbivory. For example, infested seeds of *Mimosa bimucronata* (DC.) Kuntze have higher phenolic contents than non-infested seeds, suggesting that this is an induced defense (Kestring et al. 2009). Another strategy is to only protect the part of the seed that is important. In subtropical oaks, a higher concentration of tannins at the apical half of the acorns, near the embryo, increases resistance to seed herbivory (Xiao et al. 2007).

Herbivores have evolved detoxification and sequestration mechanisms to deal with host defenses. Physical defenses, once breached by specialists, can allow access by generalists (see Sect. 16.4.3), but chemical defenses continue to operate even if a specialist gains access, thus reinforcing the specialization of reproductive structure herbivores. For example, *Curculio* performance in different acorn species is determined by the chemical composition of the acorns (Munoz et al. 2014); access by one species does not allow access by others. Similarly, Janzen (1969) found that dry tropical hardwood legumes use a wide range of chemicals for defense against bruchid beetles, including pentose, methylpentose, saponins, endopeptidase inhibitors, alkaloids, and free amino acids. The latter group frequently accounted for host specificity (see Sect. 16.4.3).

16.3.1.3 Physical Defenses

There is considerable evidence that herbivory acted as a selective agent in the evolution of many physical traits of reproductive structures. Fossil records show an increase in seed cone size and compactness (percent of interlocking scales) in Cupressaceae and Pinaceae species during the Early to Middle Jurassic (Leslie 2011). During the same period, insect mouthparts show significant diversification (e.g. the appearance of new piercing and sucking types) and new insect groups such as weevils emerged.

Since the number of seeds per cone did not increase with size, and pollen cones, which are less susceptible to herbivory, remained similar during the same period, the increase in cone size suggests a greater investment in protective tissue in response to increased severity and diversification of seed herbivory.

Seed coat toughness is another form of physical defense, such as is found in the pericarp of the baobab tree. The baobab weevil is one of the few insects capable of breaching this defense system (Lukasic and Johnson 2007). Another physical defense is resin, which frequently kills eggs and larvae, especially in conifers. For example, *Pinus cembra* L. is unique among European conifers in successfully defending against the pine cone weevil, *Pissodes validirostris* Gyll. by copious resin flow during moist conditions (Dormont and Roques 2001).

Other physical traits may have been selected by herbivory such as the number of seeds per structure, seed size and seed coat thickness (Fenner et al. 2002). For example, the large seed mass and early (i.e. autumn) germination of subtropical oak species, provide some tolerance for partial consumption of the seed without totally preventing germination and even the establishment of a viable seedling (Xiao et al. 2007). The number of seeds per reproductive structure may also be under selective pressure from herbivory. Seifert et al. (2000) found indications of an interaction between the seed quantity in spruce cones and seed insect infestation. On the contrary, no correlation was found between the total number of seeds in a cone and their infestation by the seed wasp *Megastigmus suspectus* Borries (Skrzypczynska 1998).

Lignification of the reproductive structure or the presence of a waxy surface are other physical defenses that may make it hard for herbivores to oviposit inside or at the surface of the structure. Lignification will generally occur progressively during the development of the reproductive structure. For herbivores that oviposit inside the reproductive structure (e.g. endophytic seed feeders, see Sect. 16.2.3.2), oviposition success will be primarily linked to their ability to penetrate through the tissues as they harden. Often, hardening is accompanied by intensive structural changes that render oviposition possible for a narrow temporal window so herbivores have to synchronize their development with the phenology of their hosts.

When physical defenses are breached, it is usually by specialist species, which then allows access to reproductive structures by generalists. For example, in many leguminous trees, a single specialist species can breach physical barriers, which allows entry of multiple non-specialists (Meiado et al. 2013). Thus, the failure of physical defenses can result in a complete defense breakdown.

Selective pressure exerted by reproductive structure herbivores may be countered by selection pressures from a variety of other sources. For example, selection for smaller seed in response to seed herbivores might be countered by the advantage larger seeds provide to the seedling. Physical characteristics of reproductive structures have also influenced the evolution of herbivores. For example, seed size appears to be an important selective agent in the evolution of rostrum size in acorn weevils (Hughes and Vogler 2004).

16.3.1.4 Ontogenetic Defenses

Seed ontogeny can be broadly divided in two groups. In most angiosperms and some gymnosperms (e.g. Cupressaceae), the accumulation of nutrients in the megagametophyte (conifers) or endosperm (angiosperms) occurs only if pollination and fertilization were successful. In other gymnosperms (Pinaceae and Cycadales), the accumulation of nutrients is independent of fertilization and sometimes pollination. Recent histological studies suggest that the endophytic seed feeders of the genus *Megastigmus* synchronize their oviposition to the onset of nutrient accumulation during seed ontogeny (Boivin et al. 2015). More specifically, in a Pinaceae/*Megastigmus* system, the wasp oviposits early during megagametogenesis, a stage at which intense cell death results in the production of a mucilage-like matrix rich in polysaccharides and proteins. In addition to targeting an early phase of the seed development, this seed wasp can redirect ovule development to prevent the degeneration and death of unfertilized ovules and induce the accumulation of nutrients used as food resource for the developing larvae (von Aderkas et al. 2005). In comparison, species parasitizing Cupressaceae lay their eggs later, during embryogenesis. At this stage, a corrosion cavity forms by intense cell lysis of the megagametophyte, creating space for the embryo to grow. The cell lysis provides readily available nutrients to the developing larva. Thus, it appears that these endophytic wasps have evolved towards the use of a plant structure that is a natural sink for nutrients. Moreover, in an interesting and possibly new type of insect-plant interaction, post-fertilization wasps can prevent megagametophyte degeneration and induce differentiation of plant storage tissue even in the absence of fertilization. Extending their observations to a larger group of seed parasitoids, Boivin et al. (2015) suggested that these insect-plant interactions evolved from passive host exploitation when oviposition occurs post-fertilization, to active host manipulation when eggs are laid pre-fertilization, and finally to active host manipulation with creation of new host structures for gall-inducing insects.

In some instances, reproductive structures and their faunistic complement may display parallel successional stages through time. Lukasic and Johnson (2007) found that baobab fruit go through distinct successional stages, with specialist curculionids invading first, using adaptations to breach the defensive pericarp, followed by less specialized lepidopteran larvae, then generalist dipteran larvae as the attacked fruit defenses progressively degrade. *Orsillus maculatus* (Lygaeidae) attacking Mediterranean cypress waits until *Megastigmus* spp. have emerged, then uses their emergence holes for oviposition (Ciesla 2011).

Some forest trees can also defend viable seeds using “decoys”. Delayed self-incompatibility in the tropical dipterocarps (see Sect. 16.2.4) means that self-pollinated ovules, which would otherwise be non-viable, are maintained for a period of time. Thus, insect herbivores might target ovules destined to die anyway, thus protecting a higher proportion of viable ovules (Ghazoul and Satake 2009). This theory holds up well when modeled on dipterocarps, and generally holds for any herbivore-satiating mass-flowering forest tree species, but no data exist to verify the models.

16.3.2 Host-Finding and Selection

According to the preference/performance hypothesis (Thompson 1988), if the quality of sites in which an insect lays its eggs influences offspring fitness, natural selection should favor females that oviposit in high-quality sites. In obligate cone-feeding insects, the adult female selects the host, while the larvae must live with her selection (Turgeon et al. 1994). In facultative cone-feeders (inflorescence feeding guild), the larvae can also find and select vegetative structures, thus expanding their potential resource to both reproductive and vegetative structures and reducing the risk of poor host acceptability.

Host-finding is influenced by the spatial structure of forests. In temperate forests with only a few dominant species, insects can move freely between closely spaced hosts, ensuring easy host-finding. This is even more the case in seed orchards where non-host trees are eliminated. However, in tropical forests with a high diversity of tree species, the hosts of any given herbivore species tend to be distributed as islands of widely spaced individuals, separated by a sea of non-hosts. This leads to difficult host-finding and high mortality during the host-finding stage (Janzen 1971).

Cues used in host finding are both long- and short-range. Adults of obligate conifer cone-feeders tend to use whole-tree cues (visual or chemical cues) for long-range orientation, and cone cues (primarily chemical) for short-range orientation (Hulme and Benkman 2002), whereas adults of non-obligate cone-feeders use both whole-tree and cone cues for long-range orientation (Turgeon et al. 1994).

Host finding cues have been explored with many species, and include:

- Chemical cues: These are volatile compounds that can function as long- and short-range cues, and surface chemicals for short-range cues. They are usually attractive, such as the spruce cone terpenes α-pinene, β-pinene, and myrcene that attract *Cydia strobilella* (Jakobsson et al, 2016). However, repellent compounds can also guide long-range orientation. Bedard et al (2002) found that certain repellent non-host aldehydes, alcohols, and (+)-conophthorin also mediate host-finding in the *C. strobilella* spruce system, by repelling females from non-host trees (thus effectively steering them towards host trees). Turgeon et al. (1994) implicated terpenes as being important in long-distance host-finding. Short-distance discrimination of foliage from cones could be mediated by differences in chemicals: in *Picea*, terpinolene and aliphatic acids differ between foliage and cones; in *Pseudotsuga* it is primarily monoterpenes; and in *Pinus*, several sesquiterpenes have been identified. Whether these short-distance potential cues are actually used, though, has not been investigated. Very short distance differentiation between cone bracts and scales can be determined by terpenoid differences (Turgeon et al. 1994), but again it is unknown if these cues are used in host selection.
- Visual cues: These are used when there is a difference between cone and foliage colour. Colour cues are important in some species (e.g. *Contarinia oregonensis* in Douglas-fir, Zahradnik et al. 2012), but not in others (e.g. *Dioryctria abietivorella* in Douglas-fir and *Leptoglossus occidentalis* in western white pine, W. Strong unpublished). It has been suggested that the difference in infrared emissions by

cones and foliage is used by *L. occidentalis* in finding its host (Takacs et al. 2008), though this was later challenged by Schneider (2014).

- Shape and size of reproductive structures: Though this has been implicated in host defense and utilization, little has been found regarding host orientation. Zahradnik et al. (2012) found that branch-shaped (long and thin) but not barrel-shaped (short and wide) silhouettes are attractive to *C. oregonensis*, possibly indicating that branches are used in orientation towards the cone-bearing portions of Douglas-fir.

Host-selection following host-finding requires a means of assessing host quality. Bruchid beetles in tropical legume forests probably select hosts based upon the types of alkaloids and free amino acids present (Janzen 1969). These are very toxic compounds that are present in different types and quantities in different tree species; each species of bruchid has evolved to cope with the chemical suite in a restricted host range. Some of these cues can be co-opted for mate finding: *Cydia strobilella* males (but not females) are frequently caught in traps baited with volatiles specific to their spruce hosts (Jakobsson et al. 2016), suggesting that they use the volatiles to find mates or locations where mates are likely to be.

16.3.3 Temporal Transience

16.3.3.1 Within Season

Reproductive phenology (i.e. the seasonal onset and the duration of the different phases of reproduction) of individuals of the same host species can vary broadly among populations depending on local conditions, suggesting that these traits can evolve rapidly in response to bottom-up selective pressures such as climate and photoperiod. Top-down selective pressures such as biotic interactions may also affect the selection of the onset and duration of flowering period depending on the nature of the interaction (mutualist vs antagonist, Elzinga et al. 2007). Two types of flowering phenology can minimize predispersal seed herbivory. One strategy is to desynchronize flowering with herbivore phenology, i.e. producing fruits before or after seed herbivory peak. The opposite strategy is to apply ‘herbivore satiation’ (Janzen 1971). In this case, fruits are produced in massive quantities over a short period of time so that the herbivore cannot manage to attack all of them. However, escaping herbivory in time can have negative selective consequences. Flowering might occur during suboptimal periods such as times when fewer pollinators or seed dispersers are available, or times when frost or drought can impact seed production.

In some conifer species, the timing of reproductive structure infestation seems to depend on the lifestyle of the herbivore. Obligate cone-feeders prefer the middle stages of cone development, which have high sugar content and low indigestible fiber levels, while facultative cone-feeders prefer early or late stages, which might have nutritional characteristics more similar to the foliage they also feed on (Roques 1991).

Finally, the timing of attack with regard to the host reproductive phase may affect the outcome. For example, *Megastigmus* species that attack Cupressaceae oviposit only after ovule fertilization, while those that attack Pinaceae can exploit the host before or after fertilization (Rouault et al. 2004). Thus, the Pinaceae group can parasitize a higher proportion of ovules. In another example, the synchrony of acorn production and acorn weevil larval growth has implications for the success of regeneration. When phenological synchrony is good, fewer acorns survive to maturity and canopy recruitment suffers, while asynchrony leads to improved oak reproduction (Munoz et al. 2014).

16.3.3.2 Between Seasons (Masting)

The reproductive pattern of many tree species is characterized by high annual variability and spatial synchrony. This phenomenon, referred to as masting or mast seeding (Silvertown 1980), manifests itself in intermittent and synchronous episodes of abundant reproductive structures (mast years) followed by one or more years of low abundance (non-mast years, Kelly 1994). The mechanisms involved in mast seeding have been debated for many years. According to Poncet et al (2009), three conditions are required for masting to be successful: mast year crops must exceed the consumptive capacity of the herbivores; mast years must be separated by sufficient time to reduce herbivore numbers between mast years; and mast crops must be synchronized over a greater spatial scale than the herbivore dispersal distance. Linhart et al. (2014) clarifies Poncet's first condition as a requirement that the herbivore must follow a Type II functional response, in which the proportion of reproductive structure consumed declines with reproductive structure density, due to satiation.

From an evolutionary point of view, several lines of evidence support the theory that herbivory favored the selection of spatial and temporal variation in reproductive structure dynamics, particularly large-scale reproductive synchrony (masting) that leads to herbivore satiation (Kelly 1994). Models that combine masting and herbivore population dynamics have been used to investigate the role of herbivores in selection for mast fruiting. Surprisingly, even if masting is often considered as the most common strategy to escape herbivory, results show herbivory is not required for masting to evolve. The presence of seedling banks with some seedlings surviving more than one year is required for masting to develop (Tachiki and Iwasa 2013). In the absence of this condition, even strong herbivory does not in itself promote masting. When multi-age seedling banks are available for recruitment to fill forest gaps, herbivory can promote the evolution of masting.

Although the theoretical framework for the role of masting in herbivore satiation is now well developed, there has been limited empirical evidence to support it until the recent publication of several long-term studies. In a 17-year study, Poncet et al (2009) found that European larch cone crop size was synchronized across a wide region in the French Alps. Low seed predation by a species complex of the highly mobile cone-tunneling *Strobilomyia* (see Sect. 16.2.2.2.1), in years of low cone crops following mast years, supported the satiation theory (Fig. 16.2). A high rate of reproductive synchrony was also found in a 29-year study of ponderosa pine (Linhart et al. 2014) (Fig. 16.3), as well as a Type II functional response and higher overall predation (but lower proportion of seeds consumed) in mast years (Fig. 16.4). Lower predation rates on individual trees with more cones in mast years suggested the intensified effect on insects with lower dispersal capabilities. Kobro et al. (2003) found that fruit production in the rowan tree, *Sorbus aucuparia* L. (Rosaceae) was synchronized spatially and temporally over the course of a 22-year study. The apple fruit moth *Argyresthia conjugella* Zeller used apple during years of low rowan fruit production, which reduced the success of masting for rowan trees. In the same system, an earlier study (Sperens 1997) found a type II functional response, with more moths in high fruit years but a lower proportion of damage. However, masting was determined to be less effective because tree populations were small with high local synchrony but poor regional synchrony, and moths are highly vagile.

Other examples of the effect of temporally variable production of reproductive structures on herbivore satiation have been observed in Mediterranean oaks (Espelta et al. 2008), European juniper (Mezquida et al. 2016), Antarctic beech (Soler et al. 2017), Japanese beech (Yasaka et al. 2003), European rowan (Żywiec et al. 2013), Japanese oaks (Fukumoto and Kajimura 2011) and American ponderosa pine (Linhart et al. 2014).

Masting is generally most successful against host-specific obligate cone, fruit, and seed feeders (Hulme and Benkman 2002). Herbivores with a broad host range can feed upon reproductive structures of alternative tree species during non-mast years. Non-obligate feeders can survive low crop years by feeding on vegetative plant parts, such as western spruce budworm on Douglas-fir (see Sect. 16.2.1). Less

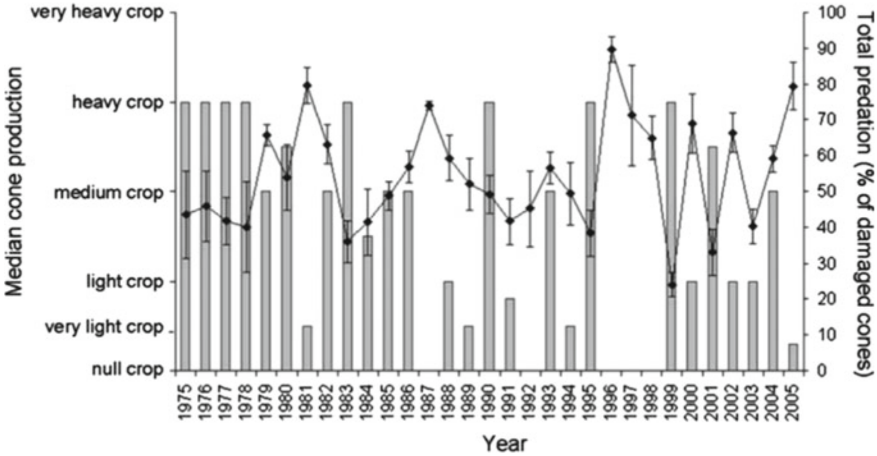

Fig. 16.2 Annual fluctuation of cone production in European larch in the 20 sites studied in the French Alps (*bars)* and of global predation rates by *Strobilomyia* species (*circles*; mean ± SE). In 1987, 1992, 1996, 1997 and 1998, the median larch cone production was nill but enough cones were sampled to calculate a predation rate. From Poncet et al. (2009)

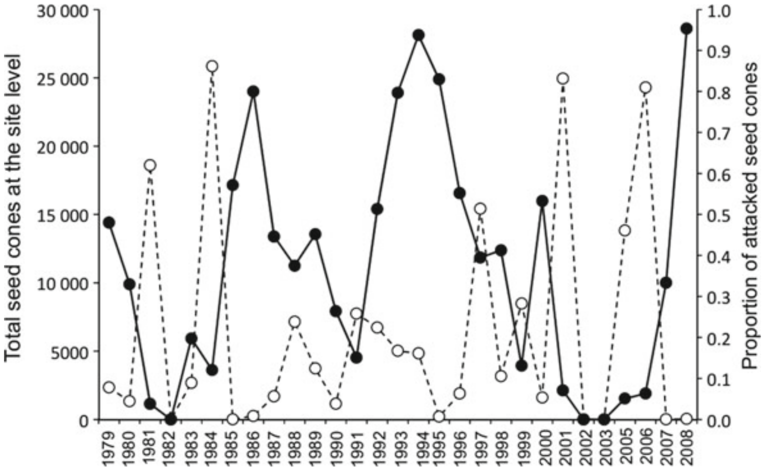

Fig. 16.3 Annual estimates (from 1979 to 2008, except 2004) of the total number of seed cones at the site level (white dots, dashed line and left axis) and proportion of attacked seed cones by specialist insect seed predators (black dots, solid line and right axis). Each point represents the average of 217 ponderosa pine trees. Error bars are omitted for clarity. From Linhart et al. (2014)

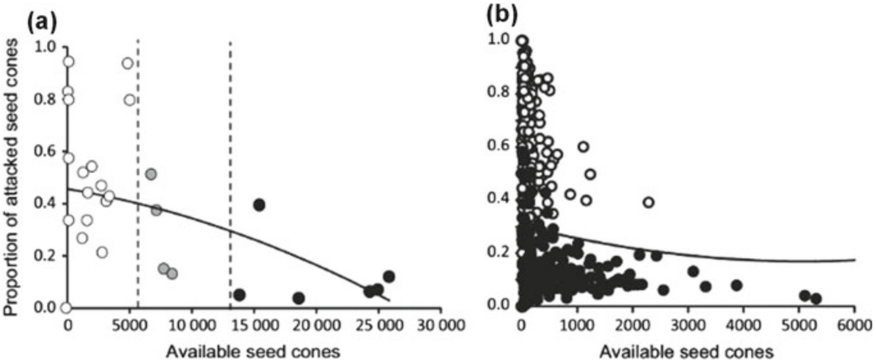

Fig. 16.4 **a** Relationship between the number of available seed cones and the proportion of attacked seed cones by insect seed predators at the population level (white dots for non-mast years, grey dots for intermediate years and black dots for mast years, $r = -0.44$, $P = 0.017$). Each point represents a year ($N = 29$). **b** Relationship between the number of available seed cones and the proportion of attacked seed cones by insect seed predators at the individual level in non-mast years (white dots, $r = -0.11$, $P = 0.117$) and mast years (black dots, $r = -0.20$, $P = 0.003$). Each point represents an individual ponderosa pine tree ($N = 217$). The single lines shows the functional response across all trees in both mast and non-mast years. From Linhart et al. (2014)

mobile insects are more impacted by masting because greater mobility allows insects to find widely dispersed crops, outside of the masting region. This can be particularly relevant in obligate, host-specific seed-feeders with high mobility. The timing of reproductive structure herbivory within a year can also be important in the success of masting. Harris et al. (1996) found that pecan nut casebearer, *Acrobasis nuxvorella* Neunzig, which attacks seeds early in the year, lives at low densities and feeds on the few nuts produced in non-mast years, thus reducing nut density to zero. The pecan weevil (see Sect. 16.2.2.1.2), which feeds in later season, must then deal with intensified masting effects (i.e. very low nut availability in non-mast years).

Forest structure is important in the success of masting as well. Tropical forests with widely separated individuals of a species can use masting successfully against obligate specialists because of the difficulty of locating and moving to another individual of the same species (Janzen 1971). Tropical generalist insects are less affected by masting because of the ability to use other tree species or plant parts. Masting in temperate monoculture forests is often less effective, particularly against insects of high mobility, because of the ease of finding and moving to non-masting hosts, perhaps outside the masting area. In this way, as host density increases, herbivore satiation becomes less effective.

Herbivore satiation in the absence of masting is another defensive mechanism. Dry tropical *Acacia pennatula* (Chamb. and Schltdl.) Berth. produce abundant seed in mid-altitude areas where seed production is greatest and energetically least costly; this satiates seed-feeding bruchids (*Mimosestes* spp.) and ensures the preservation of some seeds (Peguero et al. 2014). On the other hand, in high-altitude areas where seed production is more energetically expensive, *A. pennatula* uses seed abortion: the tree aborts seeds upon bruchid oviposition, thus allowing the diversion of energy to uninfested seeds, and decoying the bruchids into a reproductive dead-end, thereby reducing insect numbers.

Janzen (1969) found that different dry tropical *Acacia* spp. responded to feeding by bruchids in one of two ways. Some species produce more total weight of smaller seeds that have reduced defensive chemicals, resulting in herbivore satiation allowing a few escapes despite high seed mortality. Other species produce a lower total weight of larger seeds, with moderate or high levels of defensive chemicals, resulting in low seed mortality and a higher percentage of escapes. Herbivore satiation is aided by spatial discontinuity of the trees, thus favouring high production of small seeds. Satiation is hindered by a greater number of bruchid species feeding on one tree species, which encourages lower production of well-defended seeds.

16.3.4 Evolutionary Consequences at the Host Species Level

While reproductive structure herbivory has considerable impacts on host seed output (Crawley 1989) it is less clear how strong a selective force it is in shaping host tree reproductive and non-reproductive traits. In general, trees produce far more immature ovules than can possibly mature, the loss of some to herbivory might not affect host fitness. Even if the host's capacity to produce seeds is reduced, other factors may compensate, such as an increase in maternal resources or a decrease in seedling competition. To affect evolutionary trajectories, reproductive structure herbivory has to meet the following conditions: (1) herbivory rates have to consistently relate to certain plant phenotypes (e.g. plant height, shape or color, flowering phenology, number of flowers, seed size), (2) these phenotypes have to be heritable, (3) plant trait-fitness relationships have to change as a result of herbivory, (4) the magnitude of the herbivory has to be large in comparison to the sensitivity of overall plant population performance to changes in seed production. Although the data are still sparse, the overall pattern of reproductive structure herbivory suggests that the main conditions for selection are present, and a growing number of studies confirm the selective forces of reproductive structure herbivores and their role in the evolution of traits (Hulme and Benkman 2002; Kolb et al. 2007).

Assuming that herbivory meets the conditions listed above, it has likely selected for plant traits that tend to minimize the negative effects of seed loss and for plant tolerance mechanisms that do not preclude seed consumption but reduce seed loss among seed crops. In a review of the ecological literature, Kolb et al. (2007) found that the most common traits affected by seed herbivory are the number, morphology and size of reproductive structures, flowering phenology, plant size and flower number. The strength and the direction of the relationship between a plant phenotypic trait and reproductive structure herbivory is generally species dependent. For example, seed herbivory was related to flowering phenology in 80% of the species reviewed by Kolb et al. (2007) but the direction of selection depended on the species. In some cases herbivory selected for early flowering, in other cases for later flowering. Conversely, since the generation time of reproductive structure herbivores is generally much shorter than their host, it is expected that the herbivore will likely be able to track the evolution of host traits.

16.3.5 Evolutionary Consequences at the Community Level

Associational resistance exists in many plant species. This is the close spatial association of hosts with non-hosts, which increases volatile diversity and reduces the host-finding ability of pests (Barbosa et al. 2009). Though this is a common phenomenon in general plant resistance, no papers concerning this mechanism were located, which are specific to insects of reproductive structures.

Reproductive structure herbivory can play an important role in the dynamics of plant populations by limiting seed production. At the community level, interspecific differences in reproductive structure herbivory may influence the relative recruitment and ultimately the abundance of co-existing species. Specifically, the coexistence of tree species sharing the same habitat may be maintained by differential temporal or spatial variations in reproductive structure herbivory that counteract competitive exclusion (Hulme 1996). For example, Espelta et al. (2009) studied predispersal acorn herbivory of two co-occurring weevil species on the Mediterranean oaks, *Quercus ilex* L. and *Q. humilis* Miller, and compared the relevance of this herbivory to that of other processes involved in recruitment. Herbivory significantly contributed to inter-specific differences in recruitment relative to other factors such as post-dispersal herbivory and germination. Herbivory rate cannot be used as a surrogate for the effects on plant fitness or population dynamics as there might not always be a direct link between seed herbivory, seed abundance, and recruitment (Kolb et al. 2007). In some cases, high seed herbivory rates may even enhance seedling survival by reducing post-dispersal intraspecific competition (Halpern and Underwood 2006).

Among all sources of herbivory, reproductive structure herbivory can be of particular importance because of its direct and obvious impacts on plant fitness and often strong effects on recruitment patterns. The Janzen-Connell hypothesis illustrates this concept: the high diversity of tropical rainforest trees is explained by the spatial variation in species-specific seed and seedling herbivores (Janzen 1970; Connell 1971). Under this hypothesis, insect herbivores of reproductive structures may promote the stable coexistence of different tree species because these insects are often specialized on a single host species and are more prone to depress recruitment of locally abundant species, thus giving advantage to rare species. The Janzen-Connell hypothesis also states that for reproductive structure herbivores to play a role in the maintenance of biodiversity, they must cause positive distance- or density-dependent mortality (i.e. mortality increases with host density). These conditions are in direct opposition to the herbivore satiation hypothesis that requires negative density-dependent mortality. However, both processes may act simultaneously at different scales. In an investigation of East Asian oak, *Quercus serrata* Thunb. ex Murray acorn herbivory, Xiao et al. (2016) observed that overall herbivore satiation limited the occurrence of Janzen–Connell effects but also that the direction and magnitude of density-dependent seed herbivory by host-specific insects differed between individual tree and tree population scales.

Reproductive structure herbivores that are not species-specific may also link the dynamics of host species that are not otherwise competing for resources. This form of herbivore-mediated interaction is known as apparent competition (Holt and Lawton 1993), and occurs when different host species share the same herbivore. Shared reproductive structure herbivores may especially reduce the occurrence of congeneric host species at close proximity as those are more likely to host shared herbivores (Lewis and Gripenberg 2008).

16.4 Diversity in Insect Strategies and Community Structures

With a rich and varied resource comes many strategies for its exploitation by insects. Competition, plant protective strategies, and spatial and temporal heterogeneity have led to distinct structuring of the insect community.

16.4.1 Species Diversity

A wide range of insect species have specialized on reproductive structures of trees. Sam et al. (2017) reared 122 species of Lepidoptera alone from the fruiting structures of 326 woody plant species. In general, host specificity was low: 69% of species attacked hosts from >1 tree families, and only 17% were monophagous. Each kg of fruit contained an average of 0.81 generalists, and only 0.07 specialists (defined as feeding within a single host genus).

Most of the community diversity studies have been conducted in the tropical Dipterocarpaceae (see Sect. 16.2.4). In Southeast Asia, dipterocarps are strictly masting host species, leading to reduced fruit herbivore species diversity (Hosaka et al. 2009). Two nanophyid weevils emerged only from immature fruit; two *Alcidodes* weevils emerged only from mature fruit, and a single *Andrioplecta* (Tortricidae) moth species was found in all stages of fruit. All five insect species were found in all dipterocarp species studied. This helps explain the evolution of synchronous mast events among congeneric host species, because if all dipterocarp species mast in the same year, then food resources are minimal across the landscape in non-mast years, thus effectively limiting populations of seed feeding insects.

Dipterocarps in Borneo, on the other hand, support a richer community of reproductive structure herbivores. Nakagawa et al. (2003) found 51 species of insects feeding on reproductive structures of 24 dipterocarp species. Herbivores were grouped into “smaller moths” and scolytids, including weevils. Feeding was non-specific, with abundant overlap in host ranges, and the dominant herbivores were not consistent among host species or among years (Fig. 16.5).

Lyal and Curran (2000) examined *Alcidoides* weevil associations in 70 species of dipterocarps throughout Asia. Though many weevil species feed on a range of host species, and up to five weevil species were found in a single host species, no weevils fed on sympatric congeneric hosts. Because of this, mast fruiting can be successful, and it is found almost universally among the Dipterocarpaceae.

Looking at the community structure of acorn weevils in oaks, Govindan and Swihart (2015) found that species richness and community similarity were highest when mast production of three host tree species were in phase. Multispecies, multiseason models show that differential suitability of hosts as resources for *Curculio* created a spatial storage effect that, when coupled with a temporal storage effect induced by prolonged diapause common among *Curculio*, facilitated species coexistence.

16.4.2 Host Resource Partitioning

Insects that feed on reproductive structures are often limited by their host resources. Competition in seeds is frequent because seeds are small, finite, and of high nutritional quality (Janzen 1971). With most plant hosts, seeds are less prone to high levels of

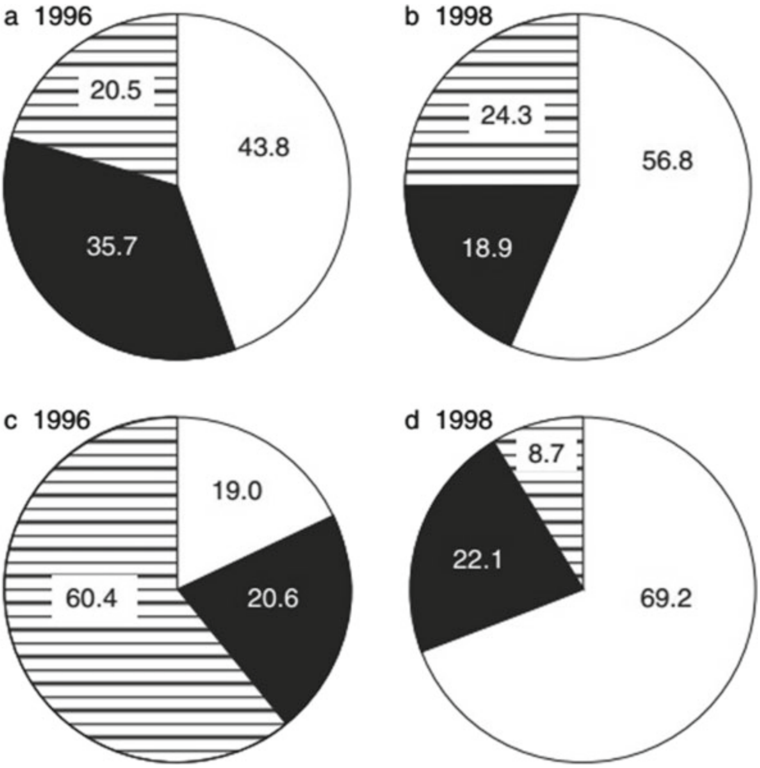

Fig. 16.5 Porportions of species (a, b) and individual numbers (c, d) of three major taxonomic groups of insect seed predators: smaller moths (horizontal bars), scolytids (solid black), and weevils (solid white), during general flowering and seeding events in 1996 and 1998. From Nakagawa et al. (2003)

herbivory after dispersal. When the bulk of herbivory is on pre-dispersal seeds, hosts tend to phenologically advance dispersal (Janzen 1971). For example, Douglas-fir, whose seeds are heavily fed upon by *Leptoglossus occidentalis* Heidemann and *Dioryctria abietivorella* Groté (see Sects. 16.2.2.1.1, 16.2.3.1), sheds seeds as soon as they are mature, while black spruce, which has few pre-dispersal pests, sheds its seeds over a protracted time period after maturity.

Phenological adjustment is not the only plant response to insect feeding pressure. Many plants have evolved phytochemicals to deter herbivory (seed escape through toxicity). These phytochemicals differ among plant structures and change as the season progresses. Thus, reproductive structure herbivores can respond by specializing, essentially partitioning the habitat in time or space, allowing a herbivore species to deal with a subset of the plant's defenses. One consequence is that habitat partitioning helps spread risk of dependence on a limited resource (Janzen 1971). Overexploitation in these situations tends to lead to contest-type competition (Atkinson and Shorrocks 1981), where multiple individuals infest a single resource unit, such as a seed, but only a single individual emerges alive. If on the other hand plants evolve high seed volumes and masting systems (seed escape through satiation), there tends to be an overlap of resource partitioning, and an increase in scramble-type competition. In scramble competition, resources are shared by all individuals, so that if resources are limiting, every individual gets less than optimal resources, leading to undersized pupae and adults, or death of all individuals in extreme cases (Atkinson and Shorrocks 1981).

Spatial division of host resources often results in a uniform, rather than random or aggregated, distribution of insects. Quiring et al (1998) found that larvae of the spruce cone fly *Strobilomyia neanthracina* Michelsen have a non-random (uniform) distribution among cones, thus reducing competition when uninfested cones are still available. This was found to be mediated through a host-marking pheromone applied by the adult female's mouthparts after oviposition. With *Bruchidius dorsalis* (Fahraeus) feeding on seeds of the Japanese honey-locust *Gleditsia japonica* Miquel, if the number of eggs is less than the number of seeds, larvae search for seeds not previously infested, giving a relatively uniform larval distribution (Shimada et al 2001). If the number of eggs exceeds the number of seeds, up to 10 bruchid larvae can feed on a single seed, but usually only one adult emerges, with no decrease in body size. This cannibalistic contest competition ensures some survival despite limited seed resources.

Studies on the bruchid beetle *Callosobruchus maculatus* (F.) have shown that two evolutionarily distinct strains exist. "S" strain adults lay only one egg per seed, and larvae resort to contest competition, whereas the "I" strain adults lay >1 egg per seed, and larvae display scramble competition (Messina 1991). These strains are genetically determined, having evolved as a consequence of the long association of the bruchid with a small-seeded host. It was found that the S strain outcompetes the I strain unless I strain larvae have a 2-day head start. Neither form can be completely overtaken by the other in competition models, a result that was confirmed and explained in the following subsequent studies. Toquenaga (1993) showed that the type of competition was density dependent, and which strain predominated depended on seed size. Tuda and Iwasa (1998) further studied the system in the laboratory and found that the initial laboratory population engaged in scramble type competition. As the population density increased, individuals with contest-type traits appeared. In a seed with multiple larvae, if one contest type was present, only it emerged as an adult, if no contest-types were present, all the scramble types emerged. After 20 generations the system stabilized: under abundant resources, the scramble type predominated, while under limited resources, the contest type was selected for. These studies show that contest and scramble competition are coexisting genetic traits within a population, and this plasticity can lead to superior overall exploitation of variable host resources.

Resource partitioning occurs not just within an insect species, but also between species. Meiado et al. (2013) found that insects feeding on the fruit and seeds of *Enterolobium* (Leguminosae) trees partitioned the resource spatially and temporally. Some species fed on the fruit, others on the seed; species that fed on only one structure attacked at discrete and separate points of time. In chestnuts, the weevil

Curculio elephas (Gyllenhal) avoids nuts previously attacked by the moth larva *Cydia splendana* (Hübner), while *Cydia* does not avoid nuts previously attacked by *Curculio* (Debouzie et al. 1996). This is very apparent on the scale of individual nuts, less so on the scale of husks (containing two nuts), not at all at a whole-tree scale or larger. In pecan, there exists a temporal division of resources among two seed-feeding species (Harris et al. 1996). The nut casebearer *Acrobosis nuxvorella* Neunzig kills young nuts, while the pecan weevil *Curculio caryae* (Horn) feeds on mature nuts later on in the season. Early feeding by the casebearer can eliminate the entire crop in a light year, which increases masting effects on the later-feeding weevil. Thus, the weevil is faced with a more variable resource environment than the casebearer.

16.4.3 Host Specificity

Insects that feed on tree reproductive structures display a range of host specificity, from generalists that feed on multiple structures and multiple host species to specialists that feed on only a single structure, with a very limited range of host species. In European conifers, about one third of cone-feeding insects can also feed on other plant structures such as foliage; the rest are obligate cone-feeders (Roques 1991). Of the generalists, most feed on cones only occasionally, when other structures are limited. These generalists also have a wider host species range than the obligate cone-feeders. None of the obligate cone-feeders is host-specific to the species level. *Megastigmus* spp., the seed chalcids, are the most host-specific group perhaps because the larva is encased in the seed capsule, in intimate physiological and hormonal contact with the ovule (von Aderkas et al. 2005). Such conditions are ideal for speciation and the development of host-specificity. Even so, different sympatric host species are often occupied by a single *Megastigmus* species, and allopatric hosts brought into contact with European hosts are attacked by European *Megastigmus*. So, there do not appear to be any examples of host specificity to the species level in cone-feeding insects, at least among European conifers.

Host specificity can arise as a result of the seed escape strategy used by tree species, including escape by satiation (in which the host produces massive crops of seeds (masting, see Sect. 16.3.3.2) that overwhelm herbivore consumption) and seed defense, both physical and chemical (see Sects. 16.3.1.2, 16.3.1.3). In general, escape by herbivore satiation leads to lower host specificity. For example, African acacia tree species with large-seeded indehiscent pods (a large stable resource) harbour more bruchid species than tree species with small-seeded dehiscent pods (a small ephemeral resource) (Miller 1996). In frugivorous lepidoptera larvae of Papua New Guinea, Sam et al. (2017) found that tree species whose fruit had large seeds and a thin mesocarp hosted generalists only, while tree species with small seeds and thick mesocarp hosted both generalists and specialists. Janzen (1969), studying legume/bruchid systems in Central America and Kansas, found that trees fell into 2 groups: (a) small-seeded, with many seeds/tree and few chemical/physical defenses; (b) Large-seeded, with few seeds/tree, but well-defended chemically and physically. The first group has a wide complex of bruchid beetles attacking them, while the second group has none. There is likely a self-reinforcing coevolutionary shift leading to the divergence of these two plant groups, resulting in each tree strategy, with its guild of seed feeders, being evolutionarily stable.

Conifer cone size and masting can also play a role in host specificity. Red pine *Pinus resinosa* cones are too small for most *Conophthorus* cone beetle species, but red pine cone beetle *C. resinosae* lays smaller clutches of eggs on more cones so can use the smaller cones of red pine (Mattson 1980). Red pine is also a masting species, which further limits species diversity, but *C. resinosae* can oviposit, and larvae develop, on shoot tips in years of low cone density. This adaptation allows *C. resinosae* to specialize on red pine, while other *Conophthorus* species cannot (see Sect. 16.2.2.1.1).

The chemical defenses (see Sect. 16.3.1.2) that can lead to specificity include attractants, deterrents, toxicants, and feeding stimulants (Janzen 1971). The evolution of mechanisms in reproductive structure herbivores to overcome these defenses is uncommon and specific to the chemical defense, leading to a limited number of insect species capable of exploiting a narrow range of hosts: in other words, specialists. For example, bruchid beetles have evolved resistance to the alkaloids and free amino acids of many legume tree species that are toxic to generalists. The basis of this host specificity may be bacterial symbionts that break down the toxins.

The toxicity of non-seed structures can also be a source of host selection for seed-feeding insects. Tuda et al. (2014) found that seeds of the Mimosa tree *Leucaena leucocephala* (Lam.) de Wit are eaten by the bruchid beetle *Acanthoscelides macrophthalmus* (Schaeffer). However, the bruchid will not eat seeds of the related pigeon pea (*Cajanus* spp.) even though its chemical composition is very similar to the mimosa. The basis of host selection in this case is the seed pod, which in pigeon pea contains repellents and toxicants that deter *A. macrophthalmus.*

Less commonly, host specificity can be caused by adaptation to factors other than the host tree reproductive strategy. Conifer seed chalcids, *Megastigmus* spp., often specialize on hosts based on the phenology of their reproductive structure development (Rouault et al. 2004) (see Sect. 16.3.3.1). These authors also found that chalcids infesting the Pinaceae can oviposit in unfertilized ovules, whereas those attacking the Cupressaceae cannot. These differential abilities have evolved in response to different ovule physiologies between the plant families, leading to host specialization.

16.4.4 Extended Diapause

Diapause is a means of surviving periods of low resource availability (e.g. winter). When host resources are low for a variable number of years, it can be beneficial for insects to extend their diapause by one or more years. According to Soula and Menu (2003), "[Extended] diapause allows individuals to survive when conditions are unfavorable for development and reproduction, and ensures synchronization of active stages with favorable conditions. However, diapause is associated with both metabolic (consumption of energetic reserves without feeding) and reproductive (missed reproductive occasion) costs." Therefore, the benefits of extended diapause must exceed costs for it to evolve. In other words, overall fitness must increase due to extended diapause or it will be selected against.

The benefits of extended diapause are greatest when crops of reproductive structures are temporally non-uniform. Hanski (1988) found that conifer seed feeders have evolved extended diapause on host species with highly variable cone crops, but not on host species with more temporally uniform cone crops. For example, *Megastigmus spermotrophus* in Douglas-fir (which has highly variable seed production) makes use of extended diapause (Roux et al. 1997), while *M. specularis* on *Abies sibirica* (which has uniformly moderate crops through time, and virtually no crop failures) does not.

Diapause that is highly synchronized with host masting might mitigate the effects of masting on herbivore populations and increase the proportion of the resource consumed in mast years (Janzen 1971). However, synchronization can be difficult for herbivores to achieve, particularly with host species (e.g. some oaks and conifers) that initiate flower development 2–3 years prior to seed maturation. In tropical forests, synchrony tends to be reduced due to the high species diversity of trees and a lack of environmental synchronizing cues, though local or seasonal synchrony might develop. Larval densities typically do not affect diapause length, though inverse correlations between larval density and current and subsequent cone crops can be strong (Turgeon et al. 1994).

Researchers have described several kinds of extended diapause. Soula and Menu (2003) identified three evolutionary models, while Hanski (1988) described four different kinds of extended diapause in insects. All seven models can be classified to two general types: stochastic (in which the insect responds to cues that do not influence tree reproduction) and predictive (in which the insect responds to the environmental cues responsible for initiating tree reproduction) (Menu and Debouzie 1993). Turgeon et al. (1994) found that 55% of obligate conifer cone-feeders in Western Europe are capable of extended diapause. The majority use the stochastic type.

While stochastic extended diapause may not accurately predict future host resources, it can still be an effective means of spreading risk. For example the chestnut weevil *Curculio elephas*, which diapauses in the ground, has been shown to follow the stochastic type of extended diapause (Menu and Debouzie 1993; Soula and Menu 2003). After 2 years, 32% of individuals had emerged, and 56% had emerged after three years. Poor nut years, with near-zero insect recruitment, have almost no effect on subsequent insect populations, illustrating the effectiveness of stochastic extended diapause.

Stochastic diapause is also found in other trophic levels. Parasitoids of cone-feeding insects often undergo extended diapause in response to population variation in their host insects (Turgeon et al. 1994). Kobro et al. (2003) examined two fruit-feeding insects of rowan, *Sorbus aucuparia* L. Both the fruit moth *Agyresthia conjugella* Zeller and the seed chalcid *Megastigmus brevicaudis* Ratzeburg have

Table 16.1 Pooled number of seed predators and their parasitoids hatched from rowanberries in years after harvesting. From Kobro et al. (2003)

Number of years	1	2	3	4	5
Argyresthia conjugella Zeller	4873	135	20		
Microgaster politus Marsh	891	155	1	42	
Megastigmus brevicaudis Ratzeburg	1986	1809	442	106	4
Torymus aucuparia (Rodzinako)	101	196	222	57	2

Approximately 3–5 kg from each of 6 years

extended diapause that most closely fit the stochastic model. Each of their main parasitoids also displays stochastic extended diapause (Table 16.1). Such multi-trophic effects have not been found in predictive diapause.

Predictive extended diapause results in better synchrony between insect abundance and host resources, but well-described examples are less common, and the cues are typically poorly characterized. One example is *Curculio* weevils feeding on acorns in Japanese oak forests. Maeto and Ozaki (2003) report that the oaks mast every second year, and the weevils have a two-year extended diapause that is synchronized with acorn production. Predictive diapause thus allows use of an abundant resource in mast years, and avoids starvation in non-mast years. However, a failed mast event (e.g. if a late frost kills the acorn crop) can result in much lower weevil recruitment and crop damage two years later.

Some species apparently are able to use both predictive and stochastic methods, described as the stable genetic polymorphism of Menu and Debouzie (1993). The seed chalcid *Megastigmus pseudotsugae* displays prolonged diapause up to five years. Emergence after the first year of diapause is strongly correlated with the size of the seed crop that year. Because the Douglas-fir host crop size is highly variable, this component of diapause is best described as predictive. Those individuals that do not emerge after the first year emerge randomly in the following years. The proportion of chalcids that remain in diapause for up to five years are best described as stochastic. Thus, induction of prolonged diapause can be multi-factorial.

16.4.5 Natural Enemies

Due to their cryptic nature, insects of reproductive structures host few predators, but a variety of parasitoids. Parasitoids might find cryptic hosts by using a complex of volatiles, which change when reproductive structures are infested by insects (Turgeon et al. 1994). About two-thirds of Western European conifer cone-feeding species host natural enemies (Roques 1991); this is partly determined by how cryptic their larvae are. For example, when infesting shoots, *Rhyacionia bouliana* (Schiff.) has twenty species of natural enemies, but when infesting cones, only three species were found. On all cone-feeders examined in this study, sixteen families of natural enemies were found, with the parasitoid families Ichneumonidae, Braconidae, and Pteromalidae representing 76% of parasitoid species.

Cone and seed insects of Canadian tamarack, *Larix laricina* (Du Roi) K. Koch, were surveyed by Prévost (2002). One hundred percent of the cones were infested, yielding only a single viable seed per cone on average. This was despite the presence of six predators and parasitoids, indicating that natural enemies did not provide effective control of cone and seed insects. In Norway spruce in Poland, ten cone-feeding insect species were also found, and the complex had an elevational gradient (Koziol 2000). In this system some cone insect densities were reduced by natural enemies: the cone axis moth *Cydia strobilella* L. numbers were reduced by 12.3% by five ichneumonoid species; and the scale gall midge *Kaltenbachiola strobi* (Winn.) were reduced by 22.6% by six chalcidoid species. The influence of parasitoids also varied with elevation (Fig. 16.6).

Refugia play a role in natural enemy biology. Hosts can escape natural enemies by oviposition location. The cypress seed bug, *Orsillus maculatus* (Feiber), oviposits preferentially in exit holes of the cypress seed chalcid *Megastigmus wachtli* Seitner (Rouault et al. 2007). When not available, it lays eggs under scales. Eggs laid under scales are attacked more frequently by the seed bug parasitoid *Telenomus* gr. *floridanus*. Oviposition in exit holes is an adaptive strategy to escape parasitoids. Refugia also provide shelter for natural enemies. A proportion of pods of a Chilean *Acacia* tree persist over the winter; these persistent pods provide a refuge for four bruchid seed beetles (Rojas-Rousse 2006). In turn, these beetles become a refuge for four parasitoids, thus providing a mechanism for parasitoids to survive *Acacia* masting events.

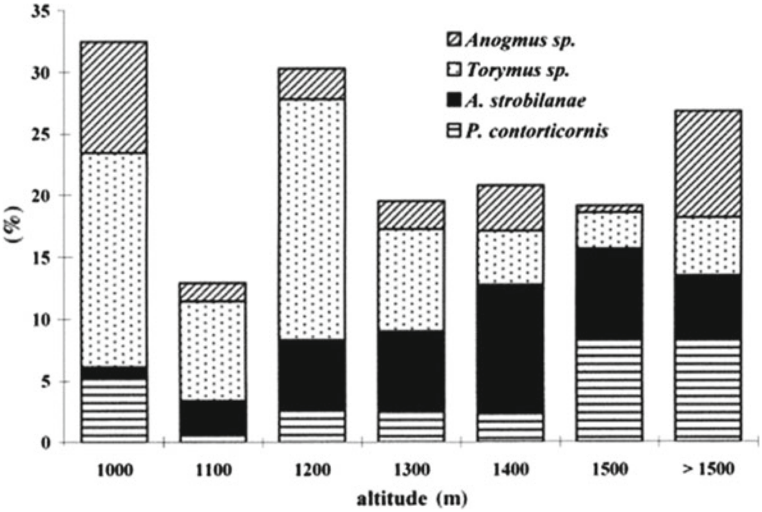

Fig. 16.6 Percentage of species from Chalcidoidea in the parasitization of *Kaltenbachiola strobi* (Winn.) at different altitudes above sea level. From Koziol (2000)

16.5 Implications for Management

16.5.1 Seed Collection in Natural Stands and Seed Orchards

16.5.1.1 Seed Collection in Natural Stands

From the early 1900's until the advent of tree improvement programs in the late 1950's, foresters collected seeds from natural stands with little concern about seed quality (Wakeley 1935). As demand for seeds intensified, seed collection areas—natural stands with undesirable phenotypes removed—provided quality seeds. Seed collection areas are chosen and managed to promote seed crops (Rudolph 1959). Collection from natural stands and seed collection areas is still the primary source for tree seeds in tropical ecosystems (Schmidt 2000). In intensively managed temperate systems, seed orchards are the primary source of seeds.

16.5.1.2 Seed Orchards

A seed orchard is a plantation of clones or progenies from selected trees. It is isolated to minimize pollination from outside sources and managed to provide frequent, abundant and easily harvested seed crops (Rudolph 1959; Zobel and Talbert 1984). Seed orchards are also used for breeding and research by forest geneticists. The intensive management includes management of insect pests and effective pest management is critical to successful orchard production (Zobel and Talbert 1984).

16.5.2 Why Management is Necessary

Management of insects of reproductive structures is seldom done except in seed orchards, seed collection stands and nut-production orchards. These insects can be devastating to seed orchards in particular. Seed orchards typically are small in area and often isolated from general forest stands. Seed orchards are monocultures intensively managed to produce large seed crops each year; this consistent, abundant and nutrient-rich resource is readily taken advantage of by opportunistic seed-feeding insects (Whitehouse et al. 2011). Genetically improved orchard trees represent years of breeding investment and resource managers want the greatest possible production of improved seed from every crop. The threshold for insect damage is low; consequently, insect pest management is necessary (Turgeon et al. 1994; Mangini et al. 2003). The situation is complicated by the fact that, for many species, the damaging stages, usually larvae, are hidden inside the cone or nut and are safe from external manipulation such as foliar pesticide application.

16.5.3 Integrated Pest Management for Insects of Reproductive Structures

Historically, seed and cone insects were controlled with routine applications of synthetic chemical insecticides with complete elimination of all insect pests as the goal. Pesticide applications included chlorinated hydrocarbons, organophosphates and carbamates, often at very high rates. For example, pine seed orchard managers in the southern United States used the organophosphate azinphos-methyl (Guthion®) to control coneworms, *Dioryctria* spp., and the leaffooted pine seed bug, *Leptoglossus corculus* (Say). Carbofuran (Furadan®), a systemic carbamate, was applied to soil under the trees. Both were effective but very toxic to non-target insects, birds and mammals.

16.5.3.1 What is Integrated Pest Management

Fortunately, resource managers have adopted an ecologically compatible approach to pest management for production of conifer and hardwood seeds and nut crops; this approach, Integrated Pest Management, can be concisely defined:

A pest management program employing the optimal combination of control methods to reduce and maintain a pest insect population below an economic threshold, with as few harmful effects as possible on the environment and other non-target organisms, and is based on: (1) the amount of damage that is tolerable, (2) the cost of reducing this damage to the acceptable level, and (3) the impact of the management on the environment (modified from Borror et al. 1989).

Integrated pest management aims to reduce injury to an acceptable level, not to eliminate the pest completely (which is rarely possible). Integrated pest management requires knowledge of the pest species present, the level of damage caused, a defined economic threshold (the number of pests that will result in unacceptable economic loss), and consideration of all possible management options (Coulson and Witter 1984; Turgeon and de Groot 1992). Integrated pest management considers the evolved interactions of host-plant and pest insect (see Sect. 16.5.5).

16.5.3.2 Integrated Pest Management Concepts

Integrated pest management requires a detailed knowledge of how the life cycle of the insect interacts with host-tree reproductive phenology. This allows the manager to focus management efforts on the most vulnerable stage in the life cycle. Small, early-instar larvae are delicate and can be killed by a very small amount of insecticide. Any life stage exposed outside the fruit, cone or seed is more susceptible than those hidden inside these structures. Exposed over-wintering stages, for example pupae or adults in fallen cones, are susceptible to control measures (see Sect. 16.5.3.5).

In managed seed orchards, it is necessary to determine if control efforts are needed and justified. Monitoring is crucial (see Sect. 16.5.3.3). This begins with estimating the impact of pests on seed yield. Historical seed yields, the estimated crop size and the value of the seeds are assessed to estimate damage thresholds based on balancing cost of control with value of the crop. The appropriate management efforts can then be taken. An effective integrated pest management strategy considers all pests present. Sometimes the methods prioritized to control the most damaging species will, by default, also control other minor pests; for example, insecticide treatments for *Dioryctria* species also impact seed bugs, *Leptoglossus* species (Hanula et al. 2002). All methods of control are considered including cultural, sanitation, biological and chemical (Turgeon and de Groot 1992).

Insecticides are still used when necessary but with proper planning and timing of applications (Turgeon and de Groot 1992). Integrated pest management also takes advantage of modern insecticides. New biopesticides, with low avian and mammalian toxicities, can be applied at relatively low rates. Growth regulators mimic insect hormones and impact only certain groups, for example, Lepidoptera. Biological agents, such as the bacterium *Bacillus thuringiensis*, are effective against Lepidoptera (Rosenberg and Weslien 2005).

When insecticide applications must, on occasion, be applied, the type of herbivory and the mode of action of the insecticide together determine efficacy. Contact insecticides, such as the synthetic pyrethroids, need only be touched by the insect to be effective; the material is absorbed through the cuticle. The growth regulators and biological agents typically must be ingested by the feeding insect; they are effective against lepidopteran larvae with chewing mouthparts that readily consume treated material. Since many insects of reproductive structures feed inside the cone or fruit, systemic insecticides, those transported through plant tissue, are potentially effective (Grosman et al. 2002; Cook et al. 2013). For example, emamectin benzoate, injected into pine trees, is effective for several years against *Dioryctria* spp. However, it is less effective against seed bugs, *Leptoglossus* spp., presumably because the material does not pass through the seed coat into the megagametophyte. Bugs, using their piercing-sucking mouthparts, are not exposed to an effective dose (Grosman et al. 2002).

16.5.3.3 The Importance of Monitoring

Monitoring of the crop and insect population is essential for effective integrated pest management in seed orchards and seed collection stands; it is an inventory control process that allows one to know the size and health of the cone crop as well as the impact of insect pests (Turgeon et al. 2005). Other benefits include identification of good and poor crop trees, identification of insect pests present, and estimation of efficacy of control measures if implemented (Turgeon and de Groot 1992; Turgeon et al. 2005). Monitoring protocols for insect damage, using traditional life-table methods, have been used for years (Fatzinger et al. 1980; Bramlett and Godbee 1982). Cones are chosen, tagged and examined at intervals as they develop. Cone condition is recorded, and crop health is determined. These protocols have been formalized into a computer-based system by the Canadian Forest Service; this includes a decision support system for managers (Turgeon et al. 2005). Pheromone-baited traps allow estimation of some insects, especially Lepidoptera (De Barr et al. 1982). Monitoring efforts must consider the extended diapause that occurs in many species (see Sect. 16.4.4).

16.5.3.4 Pesticide Application Timing

Control measures must be timed to coincide with the most susceptible host stage of the insect. This is critical for efficacy and economy, but timing is also very difficult. Insect physiology is temperature dependent; life cycle events vary with the weather from year to year (see Sect. 16.3.3.1). In the past, managers made insecticide applications at routine intervals, thus ensuring exposure to any potential pest throughout the season. Now, applications can be timed to target the susceptible stage and reduce pesticide use. For example, insecticides are often aerially applied four to six times per season to control the insect complex of loblolly pine seed orchards in the southern United States, particularly *Dioryctria amatella* (Nord et al. 1985; Lowe et al. 1994). Hanula et al. (2002) developed a degree-day model that predicts hatch times of proportions of the *D. amatella* spring-generation egg population, based on previous studies of development (Hanula et al. 1984, 1987). Two model-timed applications of the insecticide fenvalerate were as efficacious as four monthly applications for not only the coneworm but also for the seed bug, *Leptoglossus corculus*.

16.5.3.5 Environmental Manipulation

The cone beetles *Conophthorus coniperda* (Schwartz) and *C. resinosae* Hopkins are major pests of white pine, *Pinus strobus* L., and red pine, *P. resinosa* Ait., respectively. Both cause significant loss in seed orchards (see Sect. 16.2.2.1.1). *Conophthorus coniperda* adults overwinter in infested cones on the ground; *C. resinosae* overwinters in pine twigs that have fallen to the ground (Drooz 1985). Low-intensity prescribed burns in early spring kill these overwintering beetles before they emerge, resulting in reduced cone beetle attacks (DeBarr et al. 1989; Miller 1978).

16.5.3.6 Continuous Improvement of Methods

Research and new technology continually refine integrated pest management methods. Traditional management for *Contarinia oregonensis*, the Douglas-fir cone gall midge, requires insecticide application during the brief interval from conelet scale closure to conelets becoming horizontal (Hedlin 1961; Morewood et al. 2002). To assess the need for treatment, a sampling protocol using the number of egg-infested scales per conelet as an estimator of damage at harvest was developed (Miller 1986).

The method is labor-intensive and must be timed precisely and done quickly for optimal timing of treatments (Morewood et al. 2002). Gries et al. (2002) identified the sex pheromone of female *C. oregonensis*. Catches of male midges in pheromone-baited traps proved as effective as egg counts. Traps are species-specific, inexpensive and easily deployed (Morewood et al. 2002). However, pheromone-baited traps are indirect estimators of female abundance. Zahradnik et al. (2012) found that adult midges were attracted to specific infrared radiation and traps constructed to emit this radiation attract both males and females, providing a better estimate of midge numbers.

16.5.4 Seed Loss Versus Extractability

In conifers, insect feeding results in aborted conelets, cones killed or partially killed before maturity, and empty seeds. Healthy seeds that cannot be extracted from insect-damaged cones can also be a source of loss. When kiln-dried and tumbled, the scales of deformed or resin-encrusted infested cones remain closed and the seeds are not shaken out. In other instances, gall tissue or resin may fuse seeds to the scales such that they cannot be removed even if the scales open. Pre-harvest damage assessments can be done to avoid harvest of such cones (Kolotelo et al. 2001; Turgeon and de Groot 1992).

Many coarse internal feeders deform and partially kill cones. The ponderosa pine coneworm, *Dioryctria auranticella* (Groté), often causes twisted cone scales that do not open to release seed (Hedlin et al. 1981). The seedworms, *Cydia* spp., cone tunnel makers, typically do not consume every seed in a cone; however, they lay down silken threads along their feeding tunnels. This silk fuses seeds to the scale and holds them in the opened cone (Turgeon and de Groot 1992). The cone resin midge, *Asynapta hopkinsi* Felt (Cecidomyiidae), a cone scale feeder, causes distorted scales and flakes of resin that may impede extraction of host pine cones (Turgeon and de Groot 1992). Among the cone and fruit gallers, *Contarinia oregonensis*, the Douglas-fir cone gall midge, can fuse healthy seeds to scales when galls are abundant in a cone. Another cecidomyiid gall-former, *Kaltenbachiola canadensis* (Felt), forms galls in spruce cones; extraction of seeds from infested cones can be difficult (Turgeon and de Groot 1992).

16.5.5 Evolutionary Implications for Management

Stand management techniques to improve seed recruitment and forest regeneration have rarely been studied because managed conifer seed orchards have been the primary source for operational forestry in temperate areas. Lombardo and McCarthy

(2008) found that neither prescribed burns nor canopy thinning influenced seed predation or acorn recruitment in a mixed oak forest. Natural masting cycles were more influential than stand level management in oak regeneration.

Estimation of forest seed crops must take reproductive structure herbivory into account. Seed herbivory in crop estimation is particularly important in masting species. Hulme and Benkman (2002) found that specialist herbivores in masting trees cause lower percentage damage in high crop years, and higher damage in the following year. So, the proportion of seeds damaged is correlated to the size of the previous year's crop. In non-masting trees such as lodgepole pine, populations of reproductive structure herbivores can build up over time and result in an overall higher proportion of seed loss. Also, non-obligatory herbivores survive low seed years better, so they can be a greater problem in high seed years (see Sect. 16.3.3.2).

16.6 Future Perspectives

Reproductive structure herbivores and their hosts are ideal model systems for the study of many evolutionary aspects of plant–insect interactions. Because they are often highly specialized and have to rely on an unpredictable resource, reproductive structure insects exhibit a wide range of evolutionary adaptations to host detection and spatio-temporal dispersal (Boivin et al. 2017). A little-explored issue is how reproductive structure herbivory affects host populations through its effects on genetic variation in reproductive traits and the possible co-selection of non-reproductive traits as opposed to its effects on fitness. An interesting opportunity to study this particular type of selective pressure is in seed orchards where host trees are often represented by several clones, each clone having an often-well-known set of reproductive and non-reproductive traits and reproductive structure herbivory is monitored at the individual level. It is surprising that, although seed orchards constitute experimental designs well adapted to studying the impacts of reproductive structure herbivory on host genetic variation, they have yet to be fully exploited for this purpose.

Emerging anthropogenic disturbances such as climate change, land-use change and biological invasions have placed a new impetus on clarifying the ecological and evolutionary consequences of reproductive structure herbivory (Ramsfield et al. 2016). Predicted changes in temperature regimes will likely affect many insect life-history traits including diapause, developmental phenology and oviposition timing. Climate change may also affect the phenology and the interannual patterns of tree reproductive dynamics. The consequences for reproductive structure insects that rely generally on a close synchrony between their developmental phenology and the reproductive phenology of their hosts is the likelihood of a partial or total desynchrony between the herbivore and its host (Parmesan and Yohe 2003; Voigt et al. 2003). As a result, insects may exert a selective pressure on new host traits such as early reproductive phenology. The ecological and evolutionary consequences of such changes for the host populations are largely unknown. Climate change also has considerable potential to modify the masting patterns, particularly when the cue for masting is climatic. Changes in climatic drivers of inter-annual reproductive synchrony might therefore lead to a more regular production of reproductive structures. It would likely have strong effects on specialized herbivores and ultimately on the host's natural regeneration. This potential impact is of particular concern for endangered tree species with poor natural regeneration success (Guido and Roques 1996). Reproductive structure herbivory may also hamper adaptation strategies such as assisted migration by limiting seed orchard production and natural regeneration when tree hosts are at or beyond the limit of their natural range (Zocca et al. 2008; Jameson et al. 2015).

The rapid change in climatic conditions that is expected to occur in the coming decades provides a unique opportunity to observe ecological and evolutionary changes in plant–insect interactions. Although reproductive structure herbivores are often less conspicuous than other forest pests and, as such, have historically attracted less attention in climate change studies, they will constitute a key driver in the future evolution of natural and managed forest ecosystems.

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