

Chapter 2

Insect Responses to Fires

2.1 Introduction

A very wide range of insects and other invertebrates are affected by or, at least, exposed to the impacts of fire. Most are terrestrial, subject to direct exposure within the major arena of fires affecting ground surface and above-ground vegetation, but the impacts extend also to soil- and litter-dwelling taxa, and those in freshwater bodies that undergo changes through processes such as ash deposition, and changed exposure from loss of riparian or emergent vegetation. Few insects, whether terrestrial or aquatic, are completely immune to fire influences, and those influences may be direct or far more diffuse, as well as difficult to define, evaluate and document. Changes to aquatic environments (such as changes in water chemistry and sediment levels) from altered rates of runoff from nearby burned areas, or from ash or litter deposition, for example, may take months to years to manifest fully – but also with those changes largely inevitable.

The belief that some insects are ‘fire-adapted’ in some way is widespread, and invoked commonly in discussions of their responses, and their emulation by management. The basis of presumed fire-adapted species survival is that, even if individuals die as a result of fire, that same fire will maintain the habitat that they need, so that populations and species are expected to recover and thrive. The converse is simply that without fire, such species are expected to decline and die out, because the habitat is no longer suitable for them to persist.

Two related terms, ‘resilience’ and ‘resistance’, are sometimes confused in their usage in discussing responses to fire, as discussed by Moretti et al. (2006). ‘Resilience’ reflects recovery, so that high resilience was defined as ‘the rapid recovery of the species composition to that prior to the fire’. ‘Resistance’ was regarded by them as ‘the degree of similarity in species composition immediately (<1 year) after a fire’. Both are commonly correlated with fire frequency. Moretti et al. hypothesised that resistance should be highest in mobile groups, whilst single fires should allow for faster recovery than repeated fires. Insect responses to fire reflect both mortality

and the influences of post-fire succession. More generally, for systems in which fire is frequent, some arthropods appear to be adapted to such repeated and low intensity events: typically, their richness and abundance increase rapidly after each fire and remain reasonably constant until the next fire. In contrast, species in systems with naturally long fire intervals (of 20 years or more: Moretti et al. 2002) may react differently, with richness and abundance declining after at least 7–15 years after fire.

It has been suggested repeatedly that the resilience of individual species to fire may reflect their biogeographical history and origins, but there are few convincing tests of this belief. One involves comparison of the incidence of two co-occurring species of dominant ants across three different experimental fire regimes in northern Australia (Andersen et al. 2007), by sweep-netting within the grass layer of eucalypt woodland (defined by having <30 % canopy cover) and eucalypt forest (>30 % cover). The two species had rather different origins, and Andersen et al. predicted that their responses to fire would differ. *Iridomyrmex sanguineus* (a ground-nesting species) and *Oecophylla smaragdina* (which constructs nests in trees) overlap extensively in the region and both forage widely on ground and trees. *I. sanguineus* represents a dominant autochthonous genus in the region, diverse and common in areas subject to frequent fires, and it was predicted that its abundance should be promoted by frequent fire that maintains the preferred open habitat. *O. smaragdina*, the Green tree ant, is widespread in south east Asia and a relatively recent arrival in Australia. Andersen et al. predicted that it should decline with frequent fire. The three fire regimes compared were (1) early fires, the predominant savanna management approach of burning early (May–June) in the dry season to prevent fuel accumulation; (2) late fires (September–October), reflecting the common unmanaged wildfires in the region; and (3) unburned, with no prescribed fires and exclusion of wildfire. The burn treatments were undertaken annually for 5 consecutive years (1990–1994) with sweep samples taken each year from before the fires until afterward (1989–1995). The predicted changes occurred, but only after late season burns, a trait that Andersen et al. interpreted as need for relatively high fire intensity. *O. smaragdina* abundance decreased immediately after fire, as a direct effect likely to involve destruction of many nests in the canopy and occurred in open forest but not in woodland – so was habitat-dependent.

Resilience may also be related clearly to biological needs of taxa. In a later study on northern Australian ants, Andersen et al. (2014) showed that regional ant faunas can be highly resilient to fire, even when fire is considered a key threat to other regional biota. In the Kimberley area, comparisons of pitfall-trapped ants across sites sampled 1–4 years after fire showed no systematic variation in species richness, and no relationships between site similarity and time since fire reflected in ant community composition. Although two species of *Melophorus* were negatively correlated with time since fire, this was attributed to these being thermophilic taxa associated with bare ground and likely to decline as grass cover and litter accumulated. None of the 84 species trapped showed positive changes in abundance over time since fire.

2.2 Impacts and Responses

A generalised summary scheme to encapsulate the twin direct consequences of fire – the loss of organisms and the loss of resources – illustrates some of the causes of change in community richness and the pathways through which these occur (De Souza et al. 2003) (Fig. 2.1). It displays scenarios in which all individuals or only some individuals (most commonly of particular guilds) are affected. Some populations may then be lowered to below their critical survival levels, with the common conservation concern that already scarce or threatened species may be driven to extinction. The contrary trend may be that richness may be regained as competitive pressures are removed or reduced. Likewise, the extent of resource loss may or may not be significant, with possible consequent effects on populations. The array of possible fire impacts therefore includes (1) elimination of individuals sufficient to drive populations to extinction; (2) elimination of entire fire-susceptible groups; (3) reducing resources to levels where competition becomes important; and (4) reducing resource variety, leading to extinction of feeding specialists or increasing competition for those resources. The pathways leading to the right of the diagram, with reduced richness of assemblages and losses of specialist species are clearly those of greatest conservation concern, and this scheme also emphasises the critical relevance of resource supply.

In essence, these effects comprise three levels of impacts over time. Engstrom (2010) likened these to (1) direct or ‘first order’ effects over the short time period of up to a few weeks after fire; (2) ‘second order’ or indirect effects such as vegetation succession that are influenced by the variations in fire characteristics and affected habitat; and (3) ‘third order’ effects as the evolutionary effects of fire. The first order effects often appear the most severe – with, for example, many less mobile arboreal or other foliage-feeding insects suffering very high levels of mortality both from burning and from exposure to heat and smoke. The three major pest stick insect species that undergo outbreaks in Australia’s eucalypt forests can have their numbers massively reduced by fires, for example (Campbell 1961). However, and again in common with numerous other insects, resilient life stages may help to counter such impacts. In this example, nymphal and adult stick insects in the trees were highly susceptible, but the eggs (dropped to the ground) are likely to be relatively resistant other than to the hottest fires. Some of these phasmatids have eggs with elaiasomes that render them attractive to ants, so eggs are carried away or buried by ants: Hughes and Westoby (1992) suggested that they could be additionally sheltered from fire as a consequence, together with their specific egg-parasitoid wasps (*Myrmecomimesis* spp., Chrysididae).

Reviewing the impacts of fire on grassland arthropods, Warren et al. (1987) distinguished four ‘phases’ for consideration, as (1) pre-burn conditions; (2) combustion phase; (3) immediate post-burn ‘shock’ phase (both of these with acute impacts); and (4) the longer-term recovery phase. Different components of the arthropod community may be influenced differently – Warren et al. distinguished between likely responses of (1) flying surface dwellers; (2) non-flying surface

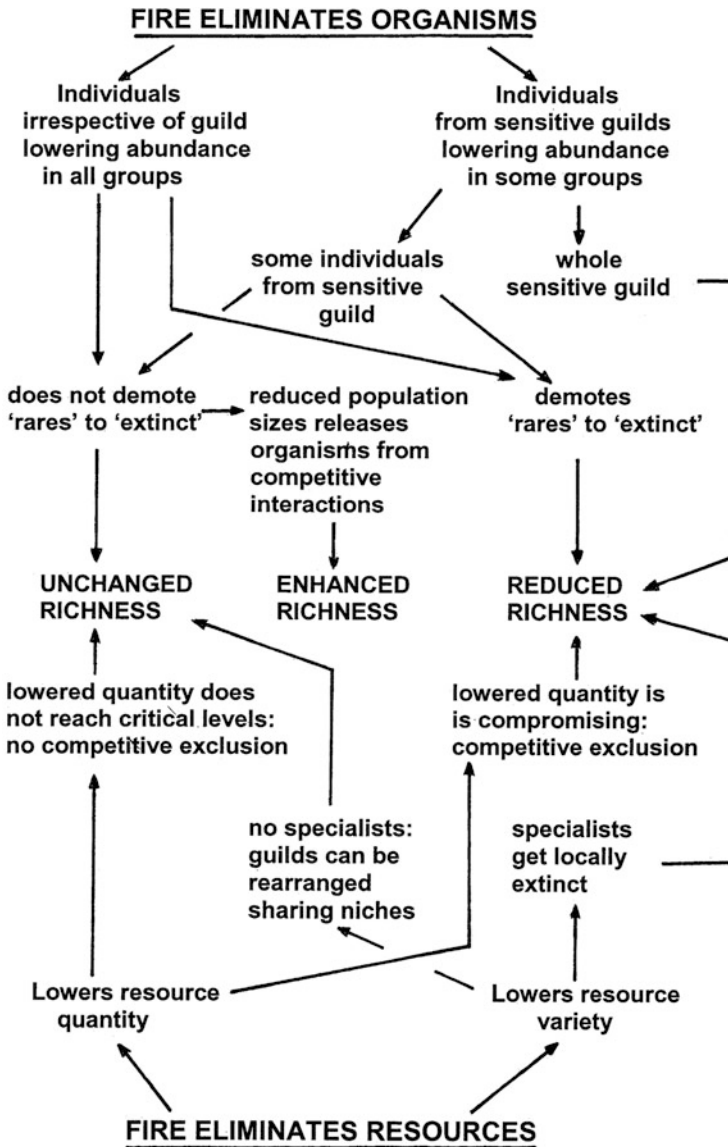


Fig. 2.1 Theoretical pathways showing how richness in communities can be changed following a fire event. *Top to bottom* shows likely pathways from elimination of individual organisms; *bottom to top* shows likely pathways from fire eliminating resources (After De Souza et al. 2003, with permission)

dwellers; and (3) soil dwellers, and these categories help to demonstrate the variety of responses, together with likely differing susceptibility of different life stages, in relation to features of the individual fire and the broader fire regime.

Very broadly, and in addition to the characteristics of the fire itself, fire has three major impacts on insects, reflecting the availability of possible refuges, the sometimes characteristic behaviour (such as dispersal) of the insects, and ecological characteristics of those insects. Direct immediate impacts may be severe, and involve large scale mortality from either or both of direct cremation and lethal heat exposure. Coleman and Rieske (2006) reiterated the term 'shock phase' for the immediate consequence of fire disturbance when, in their context of forest litter fires, leaf litter is destroyed, soil moisture and vegetation cover are reduced, and ground surface temperatures increase, each contributing to microclimate changes and habitat suitability. Relatively few workers have studied the general impacts of soil heating from fires on subterranean insects, although several specific examples of such possible refuge are referred to elsewhere in this book. A trial of exposing different life stages (eggs, larvae, pupae, pre-escape adults) of two species of ground-nesting Megachilidae bees to increased temperatures whilst they were buried in moist sand showed high survival at temperatures of 38 and 42 °C imposed for up to 27 min, but no survival at 54 °C (Cane and Neff 2011). Because surface fires often pass quickly they may sometimes have rather low impacts on insects in soil, but deep surface litter may prolong the heating phase to endanger near-surface insects, in particular. Cane and Neff suggested that bees nesting deeper than 10 cm in soil should almost always be safe from fire. They also evaluated data from the 445 bee species for which nest depth information was available, to imply that only 9 % of these species may become at risk through soil heating. Conversely, hotter fires could provide more bare ground for ground-nesting bees and others to exploit – a feature that Campbell et al. (2007) tentatively associated with increased abundance of Halictidae and related Hymenoptera on their hot-burned plots, but also noted that this outcome might reflect increased richness of understorey vegetation following burns.

During the period of the shock phase, insects continue to die from starvation and increased exposure. Direct mortality may be largely inevitable for insects that cannot move away rapidly, particularly if they live exposed on the ground or susceptible vegetation. Many such taxa are 'low profile' to managers, and have rarely been investigated, so that the real impacts are, simply, unknown. The cynipid gallwasp *Anistrophus silphis* induces galls on the wholeleaf rosinwood (*Silphium integrifolium*) in prairies of North America and larvae inhabit galls made on the plant's growing tips for an entire year as they develop. They are thus highly vulnerable to spring fires (Fay and Samenus 1993, in a study in Kansas). Many other gall formers are also present on the prairies, but mortality of *A. silphis* from a control burn was almost total. The wasp was considered susceptible to local extinctions, especially in prairies managed by annual burns. Its survival may then depend largely on spatial refuges that remain unburned. Study of a broader array of endophytic insects depending on two species of *Silphium* showed that mortality could be close to 100 % (Tooker and Hanks 2004). Many of the stem-dwelling insects were Hymenoptera and, although dominated by *Anistrophus* gall wasps, these are associated with at least eight parasitoid species. Larvae of the stem-boring beetle *Mordellistena aethiops* (Mordellidae), likewise, are accompanied by three

parasitoid species. These insects were surveyed by bagging stem samples before and shortly after burning and recording emergences; recovery was assessed from similar samples taken 1 and 3 years after sites were burned. Many of the samples indicated total mortality after fire, but apparent survival levels (all species) occasionally reached around 20 %. Later recovery suggested that the endophytic communities are quite resilient, in common with earlier findings on prairie insects (Panzer 2002), so that Tooker and Hanks’ results supported ‘judicious use of prescribed burning’; they cautioned, however, that lack of knowledge remained a problem in assessing the wisdom of that approach.

Many arboreal insects perhaps succumb more readily to fire than do epigaeic insects, unless they are capable of exploiting refuges such as holes or shelter beneath bark. In the case of non-mobile insects, even if they appear to be ‘protected’ (as for the above gall-formers, and others such as the large gall-forming *Apiomorpha* coccoids on Australian eucalypts), destruction of the insects within their galls or other cover is likely to be frequent. Numbers of *Apiomorpha* on long-unburned (for at least 45 years) and host trees burned about a decade ago did not differ greatly, with all nine local species found on both treatments. Gullan et al. (1997) suggested that fire intervals of more than 10 years would be unlikely to affect the assemblages, as long as unburned sources for colonisers were available.

Many non-endophytic insects are indeed relatively immobile, so that mortality is likely and level of exposure to fire influential. For soil-dwellers, fire severity, measured as the depth of burn, influenced many groups of invertebrates, with some comparisons of survival and recovery in small plots in clearcut, selectively cut and uncut areas summarised in Table 2.1 (Wikars and Schimmel 2001, based on Tullgren funnel extractions of soil from 0.25 × 0.25 m quadrats) to indicate the variety of responses across different taxa. The ‘immediate response’ to fire that

Table 2.1 Numbers (with SE in parentheses) of individuals of selected groups of soil invertebrates in burned (n =30) and unburned (control, n =15) plots 1 day and 60 days after fire in *Pinus* forest in Sweden (Wikars and Schimmel 2001)

Taxon	Burned			Control	
	Before	1d	60d	1d	60d
Acarina	630(110)	70(27)	290(33)	1,050(150)	1,450(230)
Araneae	6.1(0.7)	0.57(0.29)	1.2(0.3)	6.4(1.6)	2.6(0.6)
Collembola	42(12)	0.30(0.14)	1.4(0.3)	63(15)	15(4)
Coleoptera ^a					
Staphylinidae	2.2(0.3)	0.4(0.12)	0.2(0.11)	1.6(0.5)	1.8(0.5)
Elateridae	0.9(0.2)	0.37(0.1)	0.03(0.11)	1.3(0.5)	0.53(0.32)
Cantharidae	3.4(0.4)	0.33(0.15)	0.3(0.11)	3.9(0.7)	2.6(0.42)
Diptera					
Larvae	12(3)	0.67(0.18)	0.37(0.18)	10(2)	2.1(0.8)
Nematocera	1(0.3)	0.13(0.08)	0.17(0.07)	1.5(0.6)	0.6(0.34)

^aColeoptera: Staphylinidae, adults; Elateridae, Cantharidae, larvae

burned all above-ground vegetation completely was reduction to around 10 % of invertebrates on the day after the fire when compared with those captured the day before the fire. The outcome, as expected, was considerable change in abundance and assemblage composition of soil invertebrates from both initial losses and subsequent rapid colonisation by some taxa. The latter strategy depends on the survival of those taxa in unburned or differently burned areas, with the massive rapid colonisation indicating that the source was indeed unburned forests – the nearest other recently (<5 years since last fire) burned forest was more than 20 km away (Wikars and Schimmel 2001). Soil-dwelling may be an important refuge for insects during fire, as temperature rises are generally well buffered and many insects can largely avoid direct heat stress. In Brazil, prescribed cerrado fires lead to only negligible temperature increase in soil at only 5 cm depth, for example (Miranda et al. 1993). Many ants, such as the common Mediterranean region *Aphaenogaster gibbosa*, normally nest 30–40 cm deep, where no heating is likely to occur under ‘normal’ fire conditions (Lazaro-Gonzalez et al. 2013).

Soil-frequenting ants may be rather sparse. Samples by Tullgren funnel extractions in Mexico yielded only 15 species, fewer than anticipated (Castano-Meneses and Palacios-Vargas 2003). The small numbers captured still suggested that fire reduced their density and led to some changes in assemblage composition. However, other than for litter-dwelling ants, rather few studies have assessed impacts of fires on the wealth of other soil surface/litter arthropods. The severity of those effects was demonstrated by a comparison in Brazil, in which litter arthropods (using samples from Winkler bag extractions of litter from 1 m² plots) were compared across burned and unburned areas of savanna over nearly 2 years after fire (Vasconcelos et al. 2009). Species richness of some groups declined on burned sites, together with the richness of major taxonomic groups, abundance of some individual taxa and overall abundance of arthropods. Examples (Fig. 2.2) illustrate some of the patterns over that period. Trends in some taxa show strongly parallel fluctuations in burned and unburned sites (Collembola), or converge strongly towards very similar end-points after initial differences (Araneae), and the overall arthropod richness showed strong recovery after only this rather short period. Such variety of responses between both major taxonomic groups and individual species is widespread.

A thick humus layer is an effective buffer against many imposed changes to the soil-litter interface (Haimi et al. 2000), but general effects on their arthropod denizens are also varied. In some studies, the overall trends cited imply severe impacts, but lack of taxonomic penetration hampers detailed analysis beyond such general levels. Thus, the preburn ground litter of forests in Kentucky was dominated by Acari (69 %) and Collembola (20 %), with burning causing reductions of 74 % of mites over 2 study years, and 82 % of springtails after 1 year, apparently as a direct outcome of the fire (Coleman and Rieske 2006). Treatment outcomes for the taxa investigated demonstrate the low numbers of many arthropod groups present (Table 2.2), a common occurrence that, augmented by lack of knowledge of richness within each such major group, limits severely the information that can accrue from studying them.

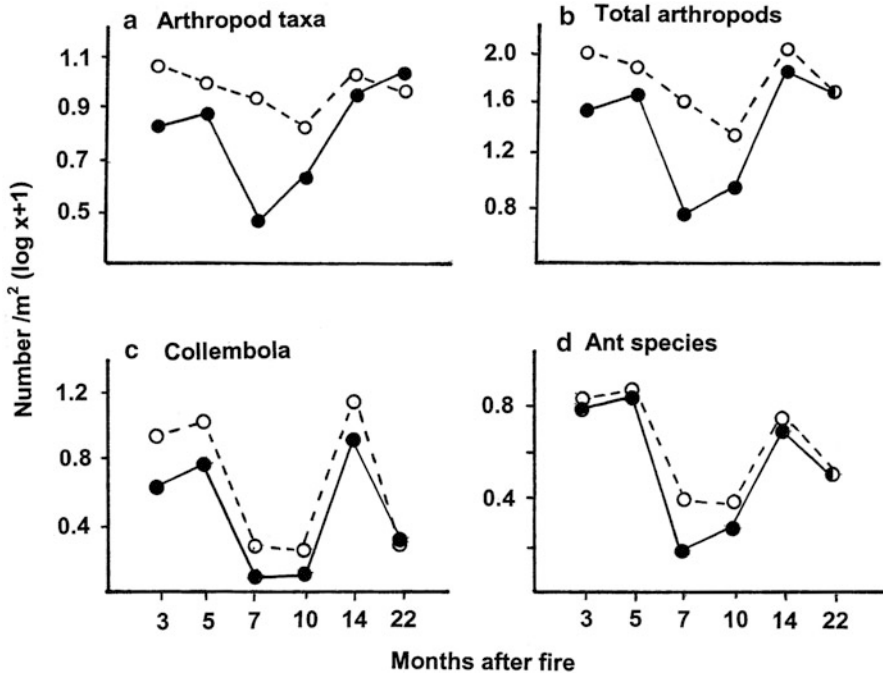


Fig. 2.2 Short-term responses of leaf-litter arthropods from 3 to 22 months after a fire, to indicate some general trends and parallels across groups: (a) arthropod taxa; (b) total arthropods; (c) Collembola; (d) ant species. *Solid circles*, burned sites; *open circles*, unburned sites (After Vasconcelos et al. 2009)

In most biotopes, even relatively mild fires can lead to substantial losses of insects unless suitable refuges are available. This outcome may be inferred across numerous taxa. Decreased abundance of a variety of litter-dwelling invertebrates from low intensity fires in Australian eucalypt forests was attributed to general simplification of the habitat structure from litter reduction and associated lessening of moisture levels (York 1999), and other parallels have been reported. Frequent such fires can have long-term consequences (Collett et al. 1993). York's results (Fig. 2.3) demonstrated considerably lower abundance and richness (at his relatively coarse taxonomic analysis level of orders) with lower litter biomass, but as York warned, this was based on only a single summer sample so its generality is unproven. In general, the samples from burned sites (with low litter biomass) contained fewer ordinal taxa and lower numbers of individuals.

However, the extents of such losses are sometimes hard to assess, particularly for stages or taxa that seem to be in some way buffered from the fire – whilst soil or dead wood may insulate insects from cremation or overheating, survival of some individuals effectively provides a nucleus for recovery, reducing the needs for post-fire colonisation. Experimental trials on saproxylic beetles (Ulyshen et al. 2010) demonstrated the difficulties of generalisation, but also the resilience of some

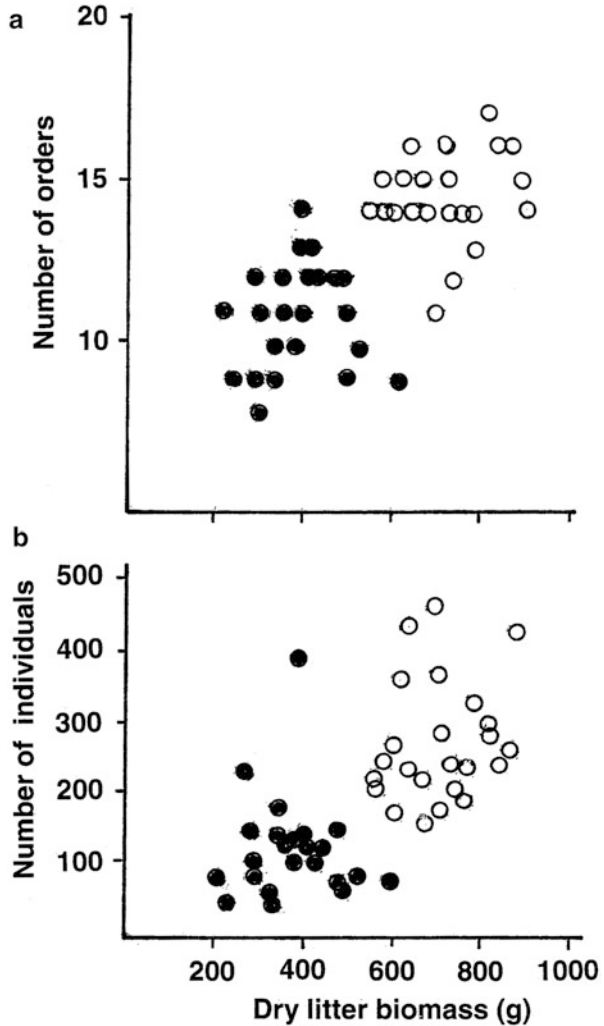
Table 2.2 Abundance (number of individuals) of selected groups of arthropods extracted from leaf litter in oak-pine forest stands in Kentucky in year of burning (2001) and 1 year later (2002). Four plots of each sampled; 'burned' includes two each of single and multiple burned plots (From Coleman and Rieske 2006)

Taxon	Burned		Unburned	
	2001	2002	2001	2002
Acari	8,138	13,825	51,008	40,234
Araneae	132	108	537	264
Coleoptera	60	66	374	233
Coleoptera larvae	119	119	465	317
Collembola	2,389	9,378	13,649	7,086
Diptera	46	40	100	54
Diptera larvae	184	334	750	444
Formicidae	417	1,213	1,053	1,225
Isoptera	47	91	4	44
Lepidoptera larvae	69	133	313	258
Opiliones	1	6	4	5
Paupoda	4	1	21	26
Protura	77	40	509	429
Pseudoscorpiones	96	139	703	446
Symphyla	32	19	94	46
All groups (including some not listed above)				
	14,582	27,816	72,427	53,501

assemblages to fire. Beetles were reared from logs, cut from dead trees and logs from the same individual tree allotted to both burn and unburn (control) treatments, of Loblolly pine (*Pinus taeda*) in Georgia, United States. The logs were later bagged, and emerging beetles collected over 5 months. More than twice the number of beetles (2,349) were reared from unburned logs than from burned logs (1,108), but 20 of the 21 most common species (those represented by >10 individuals) occurred in both regimes, suggesting that the low intensity burns used in management had little immediate impact on community composition of the log-dwelling beetles. As Ulyshen et al. commented, this preliminary survey leaves it unknown whether more intense fires might have a greater impact.

Direct mortality may be the major purpose of some planned burns, as for pest suppression (p. 148) but alternatively in conservation a major aim may be to minimise losses through designing a fire regime for greatest security of particular species or environments. Second, indirect effects occur through destruction of critical resources, most obviously food supplies or sensitively attuned microclimates, depriving the insects of livelihoods unless they are able to move elsewhere – so that area of treatment may be important. Depending on levels of exposure, such losses may be long-lasting (even, permanent) or more transient, and necessitate long term studies to elucidate the impacts incurred. And, third, fire may induce rapid dispersal of some insects to move away from the affected area. Strongly flying insects, in contrast to sedentary taxa such as gallwasps, may largely escape

Fig. 2.3 Some relationships between amounts of ground litter (given as dry biomass in grams) and numbers of orders and individuals of litter insects in eastern Australia. *Solid circles*, burned sites; *open circles*, unburned sites (After York 1999, with permission from Springer Science + Business Media)



mortality – studies on grasshoppers of the Ivory Coast, West Africa, showed that an estimated 88 % of acridid grasshoppers escaped by flying from the fire front in grassland (Gillon 1970), and were favoured by frequent burning, in contrast to many other presumed less dispersive groups (Blattodea, Coleoptera: Carabidae, Hemiptera: Lygaeidae, Pentatomidae) that were severely reduced (Gillon 1983).

2.3 Pyrophilous Insects

For completeness here, some insects respond positively or are attracted to flames or smoke, as indicators of fire increasing suitability of critical resources for oviposition or food, so that fire is a positive conditioner of their resource needs. A number of Coleoptera, most of them wood-frequenting species but also some predators such as a few Carabidae, are amongst such wellknown pyrophiles. Traits shared by many pyrophiles, and presumed to be correlated with this habit, include (1) high potential for dispersal, (2) sensitivity to respond to particular chemical or thermal signals generated through fire, (3) larval feeding only on heavily stressed or recently burned trees, and often (4) variable duration of larval development. This syndrome differs considerably from insects arriving later, the non-pyrophilous ‘secondary users’ (Saint-Germain et al. 2013) that occupy dead trees and wood in the years following initial burning. Many of these are relatively poor dispersers and have also been far less intensively studied than the rapidly arriving pyrophiles.

Perhaps the best known such species is the buprestid beetle *Melanophila acuminata*, renowned for its responses to forest fires and with specialised smoke- and infrared sensory perception (Evans 1966, 2010) enabling attraction from considerable distances – but with reports of long distances such as 150 km or 100 miles not closely documented. Even though these response distances may be exaggerated, *M. acuminata* is highly dispersive, and rapidly appears at forest fires in North America. Removal of predators and of competing wood-feeding insects may favour unhampered reproduction by this beetle in such places. Some species of *Monochamus* (Cerambycidae) can orientate using the smoke plume of fires to infest even partially burned and still smoking conifers immediately after fire. The complex interactions between beetles and fire in such northern forests have considerable importance in forest management (McCullough et al. 1998), and may influence pest outbreaks (p. 148). However, as Wikars (2002) noted, it has generally remained unclear whether the more important factor for species attracted to fire is burned wood as the actual feeding/breeding substrate or burned habitat area itself. Clarification of this could help to hone the logistics of planned burns. Some such pyrophilous taxa are scarce in, or absent from, undisturbed forests, and recently burned areas are critical for their survival (Saint-Germain et al. 2008), so that replacement of fire use in forest management by more intensive logging and clearcutting may be detrimental. The beetles noted above exemplify a much wider array of saproxylic Coleoptera (p. 106) that appear to colonise only recently burned areas so that (as Saint-Germain et al. explained) these are essential, and the species can decline if intervals between fires increase, or use of fires in management is reduced. The conservation status of many such species has proved difficult to determine.

Pyrophily is by no means limited to Coleoptera, and members of some other orders share this habit. Amongst the Diptera, some Platypezidae (notably species of *Microsania*) are known as ‘smoke flies’ through their attraction to smoke from smouldering wood. In Western Australia, they are accompanied by species of Phoridae (*Hypocerides nearcticus*) and Therevidae (*Anabarhynchus hyalipennis*),

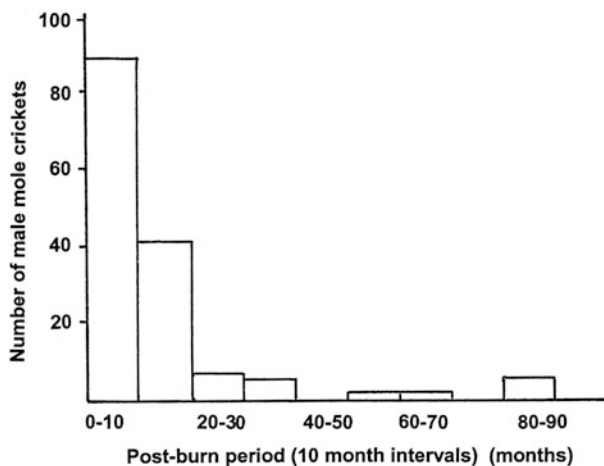


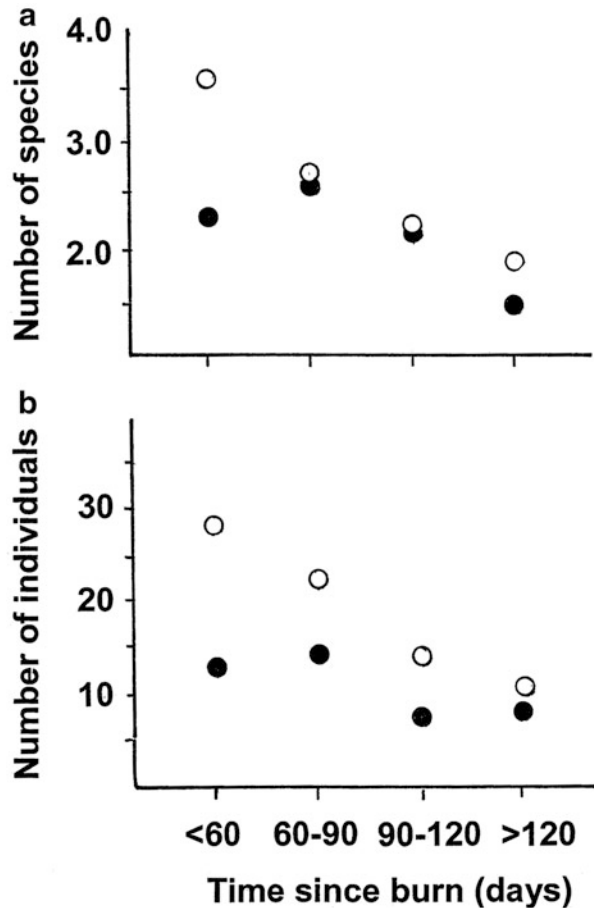
Fig. 2.4 Numbers of Prairie mole crickets (*Gryllotalpa major*) males calling aggregations in relation to time since fire (months, shown at 10 month intervals from 0) (Howard and Hill 2007, with permission)

all attracted to burned wood and soil, where oviposition occurs (Klocke et al. 2009). Their larvae are presumed to feed on fire-adapted fungi that thrive immediately after fires.

More subtle effects of fire on behaviour are exemplified by recently burned prairie sites being favoured for lek displays by males of the Prairie mole cricket (*Gryllotalpa major*) in Oklahoma (Howard and Hill 2007). Males of this species, the largest American cricket, which is regarded as rare and of conservation concern in the central southern United States, call from special funnel-shaped ‘acoustic burrows’ in the ground. Surveys in several years revealed mate-calling males in higher numbers on recently burned sites (Fig. 2.4), where some had even been observed calling within 24 h of a fire. Soil temperatures rose only little during burning, and the below-ground vegetation food was not damaged. Howard and Hill hypothesised that burned grassland sites may be more efficient for acoustic communication than more complex unburned sites with denser surface vegetation, with responding females spending less effort in discovering mates. Mosaic burning, providing such spatial heterogeneity, may be beneficial to the cricket, and it seemed clear that male *Gryllotalpa* were attracted to recently burned sites for display. Numbers declined rapidly after that initial peak.

Short term impacts are exemplified by a study of prescribed burns in the oak-hickory Ozark forests of Arkansas, and the responses of litter-frequenting ants (Verble and Yanoviak 2013). Ants were surveyed in replicated burned and unburned sites by three methods (below: tuna baiting, hand collecting, Berlese funnel extraction) from 30 to 170 days after fire, for a combined representation of 59 species. Burned and unburned sites shared 43 species, with 51 species collected in each treatment. Both richness and abundance were initially far lower on the

Fig. 2.5 Mean ant species richness (a) and abundance (b) with time since fire (days) for leaf litter fauna of the Ozark Mountains, Arkansas. *Solid circles*, burned sites; *open circles*, unburned sites (After Verble and Yanoviak 2013, with permission)



burned sites (Fig. 2.5), but the treatments converged rapidly, supporting earlier studies (such as Parr et al. 2004) that such ants seem relatively resilient to fire impacts, possibly aided by the refuge of subterranean nesting.

However, understanding behavioural changes that influence activity of insects post-fire is itself complex. General changes in activity, such as the mass ‘panic’ local flight of overwintering Monarch butterflies (p. 77) stimulated by smoke from nearby agricultural fires may be severely disruptive (Malcolm and Zalucki 1993). Foraging patterns of many insects may be influenced, for example, by several different factors such as simplified structure of the habitat (by removal of litter or vegetation), wider dispersion of food resources, and higher exposure of the insects to desiccation or predation. Loss of such buffering effects from extremes of temperature, moisture and light may also influence the spectrum of species present. Increased activity on the ground surface may be reflected in greater trap catches, and be confused easily with increased abundance. The two parameters are often

difficult to separate. For example, increased pitfall trap catches of the long-lived large predaceous carabid beetle *Calosoma frigidum* in recently burned patches of forest in northern Canada could have two explanations. Jacobs et al. (2011) favoured the option of increased activity in burned plots over any actual differences in population density on burned and unburned plots, in part because such increases were observed in the same year before any reproductive recruitment could have occurred. It seemed that fires had little direct impact on the beetles, but that increased soil temperatures linked with removal of the overlying vegetation promoted greater movement by stimulating beetles to emerge from their underground retreats. The large ‘bull ants’ (*Myrmecia* spp.) of Australia are amongst the few groups of the ‘Specialist Predators’ category of ants (p. 39), and many commonly forage on vegetation: Hoffmann and Andersen (2003) noted that changes in foraging pattern to greater foraging on the ground after fires lead to increased representation of bull ants in pitfall trap catches.

The ecological consequences of insect behavioural change from fire are diverse and in some cases far-reaching. Seed dispersal by ants (myrmecochory) is widespread, and in parts of the southern hemisphere particularly significant in dry fire-prone habitats (Berg 1975). Surveys on burned and unburned savanna plots in northern Australia compared activities of seed-collecting ants at seeds of *Acacia holosericea* placed in the field (Parr et al. 2007). Seventeen ant species (15 in unburned plots, 11 in burned plots, and representing nine genera) removed seeds. Rates of seed removal were similar before burning occurred, but dropped markedly on unburned plots after others were burned. Simplified foraging conditions contributed to increased distance of seed movement by species of *Iridomyrmex*, in particular, and Parr et al. noted this active dominant ant genus as highly characteristic of open ground habitats in the region, so this outcome might be anticipated. The syndrome of changed patterns of seed dispersal from changes in activity of myrmecochorous ants caused by fire is widespread.

Behavioural and ecological traits amongst arthropod species that can facilitate survival from burns have been assessed by both comparative examples and their extension to more general principles. Thus, Main’s (1998, p. 1) mygalomorph spider examples showed (1) the web-weaving *Cethegus* sp. with a short maturation period is more resilient to fire than the deep-burrowing *Anidiops* that takes far longer to mature, because it can disperse aerially to colonise rather than by slow walking alone; (2) some species of *Moggridgea* construct traps on tree bark, where they are susceptible to burning, whilst others burrow in soil, with impact reflecting vulnerability of the younger age cohorts; and (3) some species of Orsolobidae (*Tasmanoonops* spp.) that were lost from several different biotopes after fire had substantial ability to colonise, reaching increased numbers 4–17 years later. These relictual species have long history of association with fire, but their traits may be far more widespread.

2.4 Recovery from Fire

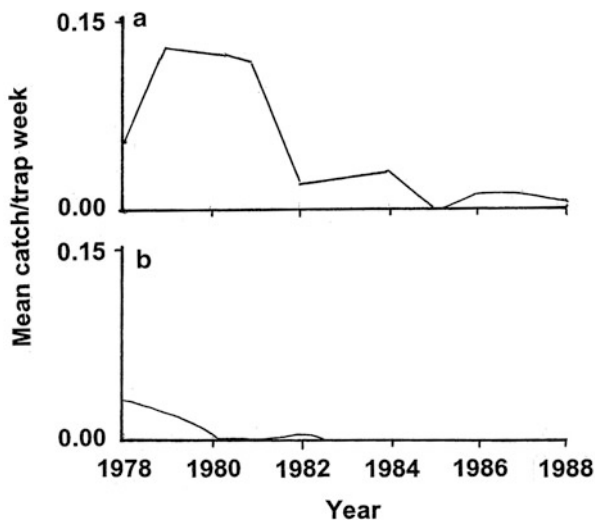
The three major general strategies of insects in adapting to fire, as enumerated for boreal forest taxa by Danks and Footitt (1989), are

1. Survival in situ, depending on local refuges such as soil burrowing, and not involving any substantial movements;
2. Rapid colonisation after fire, following local mortality or fire-induced escape dispersal; and
3. Invasion at some later stage.

Determining whether an insect population found following a fire represents survival or re-colonisation can prove complex. Some taxa, such as some wingless grasshoppers or stick insects are intrinsically poor dispersers, so that the former (from resistant eggs, p. 23) may be presumed the more likely process. However, evidence for this can be difficult to accumulate. Sandoval (2000) investigated the wingless Californian phasmid *Timema cristinae*, which occurs as a number of well-differentiated colour morphs, to assess whether relative incidence of different morphs differed in a population surveyed before a fire and 1½ years afterwards. The study area was unlikely to be colonised naturally, as indicated by mark-release-recapture trials, in which it appeared that distance from any possible re-colonisation site was considerably greater than any likely lifetime movement distance by these insects. Three indirect lines of evidence supported Sandoval's hypothesis that on site survival had occurred: (1) colour morph frequencies were very similar before and after the fire; (2) the colour morph frequencies on the burned site remained distinctive, and differed from those on the nearest possible re-colonisation sites; and (3) a unique yellow morph unknown from any other site was found again after the fire. These outcomes suggested strongly that at least some eggs survived the fire, perhaps facilitated by being covered with ingested soil at the time of laying.

Rapid colonisation parallels features of 'r-taxa' as mobile opportunists, and some such taxa have been likened to 'supertramps' (Holliday 1991, for Carabidae), some of which can exploit newly simplified environments but may not persist there as conditions diversify. Late colonisers, in contrast, have been likened to K-selected specialist species, reflecting their different dispersal propensities and ecological traits. In Holliday's (1991, 1992) surveys of ground beetles in Manitoba (Canada), the incidence of brachypterous beetles (without flight capability) and size of beetles increased with time after fire. Over 11 years, he captured almost 2,500 individual carabids, in a pool of 73 species; of these, only three were captured more frequently in burned forest sites, and 17 were more abundant in unburned (control) sites. The strategy of early recolonisation was exemplified by *Harpalus laticeps* (Fig. 2.6), abundant in both burned sites early in the study, but declining thereafter, and not found in control sites. It was the most frequently trapped species on burned conifer sites but not on aspen sites where, however, the four more abundant species were all far more numerous on control sites. Many of the species common in control sites were initially absent or rare in burned sites, suggesting that numbers surviving *in*

Fig. 2.6 Catches of the common carabid beetle *Harpalus laticeps* over 11 years in burned sites in two forest types (**a** conifer; **b** aspen) in Manitoba, Canada (After Holliday 1991, with permission from Cambridge University Press)



situ were probably low. A survey in tallgrass prairie, also in Manitoba, also confirmed that carabids responded as individual species to different fire treatments, but also that at least 4 years were needed for the assemblages to revert to pre-fire status (Roughley et al. 2010). Colonisation of burned prairie sites in Kansas occurred primarily from underground or far away, rather than from nearby sites (Cook and Holt 2006). In contrast, spring burns in remnant Illinois prairies initially lessened arthropod abundance considerably (Harper et al. 2000), but both abundance and species richness recovered quickly, before the end of summer and mostly by recolonisation from nearby unburned refuges – which were considered of critical importance for this to occur. Such cases exemplify the more general trio of fire-induced changes in insect assemblages, as (1) direct mortality of resident individuals; (2) influx of disturbance-adapted colonisers and their interactions with resident survivors; and (3) influences of successional changes over post-fire time.

Burned areas are clearly the preferred habitats of some insects, as Shapiro (1965) implied for the skipper *Hesperia metea* on North American savannas. The butterfly is associated closely with the grass *Andropogon scoparius* (sometimes called ‘fire grass’) which can become dominant on burned sites after the second post-fire year. *H. metea* continued to occur on such sites until succession led to other grasses being predominant or tree growth provided excessive shade. The control of succession by fire is a recurrent theme in insect conservation (Chap. 6). Positive short-term responses by particular insects to burns are frequently reported, but are sometimes difficult to interpret. The Marsh fritillary butterfly (*Eurodryas aurinia*, Nymphalidae) in Wales appeared to benefit from site burning, with high numbers of larval webs found on a large site burned 6 months previously (Lewis and Hurford 1997). Larvae may be able to survive ‘flash fires’ across surface vegetation, but burning also opened up vegetation that had become too dense for the larvae.

Rotational spring burning may be useful for site management for *E. aurinia*, but grazing was considered the optimal approach as overall more reliable. As another example of different outcomes, intensive or prolonged burning of peat-based mires occupied by the Large heath butterfly (*Coenonympha tullia*, Nymphalidae) in England reduced site quality, whilst low intensity patch burns had the converse effect (Dennis and Eales 1997).

Greater abundance of Carabidae in burned sites (such as in the *Pinus pinaster* forests of Spain surveyed by Fernandez and Costas 2004) is commonly attributed to arrival of opportunistic species, as above, with many of these taxa adapted to open areas. Most of those captured in control forest areas, in contrast, are more characteristic of more humid and thickly vegetated areas. As with studies of ground beetles in Poland (Zdzioch 2003), fire predominantly caused losses of true forest specialists. Any such forest fire is likely to induce a mosaic of more- or less-severely burned patches within the area affected, and within each of which different assemblages of Carabidae may persist and within which different species may be favoured. Whilst two pyrophilous carabids became predominant after fire in Swedish pine forests, *Sericoda quadripunctata* was favoured by severe burning and *Pterostichus quadrifoveolatus* was associated with weak burning (Gongalsky et al. 2003, 2008). More broadly, weakly burned areas may constitute partial refuges for pre-fire fauna. Loss of forest understorey may have drastic effects on locally endemic insects that depend on such vegetation, but both increased burns and fire suppression measures may need careful evaluation. For Portugal, Quartau (2009) cited a variety of Cicadomorpha and Fulgoromorpha (Hemiptera) that included localised endemic species restricted to a few woodland sites as amongst many taxa possibly under increased threat of extinction from forest sanitation practices, much of which is undertaken as fire prevention measures involving construction of fire breaks. A specific legal directive demands creation of mosaics with cleared areas between forest patches. Thus, (1) forest tracts greater than 500 ha should be separated by 125 m wide strips within which trees, shrubs, herbs and litter are removed, and (2) patches not bigger than 50 ha should be separated by cleared rides 10–50 m (more rarely, 100 m) wide, also with all vegetation removed. Quartau argued that this emphasis on fire prevention, with such intensive vegetation removal, is inadequate for biodiversity conservation, and that more sympathetic clearing regimes (such as maintaining well-vegetated woodland edges) would be more beneficial. Constructed and well maintained fire breaks, either from clearing of vegetation or from regular mowing or other sanitation measures may constitute important barriers or corridors to insects moving through the landscape, so may hamper or facilitate re-colonisation of sites.

Insect responses to fire also incorporate the demographic impacts on populations, often far less obvious than immediate declines in incidence but also of central concern in conservation and assessing impacts and vulnerability. However, the numerous surveys of particular insect groups in association with fires have – not unexpectedly – shown many different responses. Particular focal groups have been shown to variously become richer and more abundant or poorer and less abundant in burned than unburned ‘control’ patches. Such trends are difficult to

predict. For soil and litter invertebrates, Whelan (1995) tabulated 12 published accounts from Australia, employing various methodologies and levels of taxonomic discrimination, in which population changes attributed to fire impacts were appraised. Some showed increases, others demonstrated declines, and yet others were inconclusive or non-responding. Such correlations are rarely simple, as Siemann et al. (1997) demonstrated for Minnesota oak savanna arthropods. There, species' short term and long term responses to fire were negatively correlated. Species that were less abundant in the growing season after a spring burn were more likely also to be more abundant in frequently burned savannas, and vice versa.

2.5 The Variety of Studies

Assessing the responses of insects to disturbances, including fire, has two widespread limitations: that many studies are unreplicated and that this limits formal statistical evaluation even if the latter is considered. Many such interpretations have simply reported changes in species richness and/or relative abundance, in single sites or across treatments, without further analyses. Drawing together the different studies made in any insect group is therefore difficult, as demonstrated for ant assemblages in Australia (Hoffmann and Andersen 2003) and savanna termites (Davies et al. 2012).

Hoffmann and Andersen found fire (with 17 studies) the most frequent of the varied disturbances they appraised, and grouped ant responses into three categories: (1) weak, possibly reflecting background 'noise'; (2) apparently clear and strong; and (3) very strong. One dilemma with the first category is simply that abundance of the focal taxa may be low – as in studies of rare or threatened species, so that small changes in numbers may indeed be significant or attributed to fire. An example of low abundance cryptic ants (p. 150) is one such ambiguity. One important inference from Hoffmann and Andersen's survey was that responses of different functional groups of ants could sometimes be generalised, but were clearest when disturbance caused substantial change to habitat structure, especially to the ground layer, and least informative in very open habitats in which bare ground is already available and fire (or other disturbance) has little impact on microclimates. Three major functional group responses (terminology of Table 2.3, p. 39) were recognised, as (1) Dominant Dolichoderinae and Hot Climate Specialists prefer open environments, and are favoured by low levels of disturbance in forest habitats; (2) Opportunists and, often, Generalised Myrmicinae are broadly adapted with wide tolerances but are sensitive to competitive interactions, so their responses oppose those of the above group; and (3) Cryptic Species and Specialist Predators are especially sensitive to disturbance.

The termite studies survey (Davies et al. 2012) was necessarily more tentative: the widespread lack of knowledge of responses of Isoptera to fire and the difficulties of redressing this (Davies et al. 2010) posed problems for any attempt at general

Table 2.3 Summary of ant functional groups, based on responses to environmental disturbance and stress, formulated from Australia (Based on Hoffmann and Andersen 2003, following earlier papers)

Group and representative major taxa	Features
Dominant Dolichoderinae (<i>Iridomyrmex</i> , <i>Anonychomyrma</i>)	Abundant, active and aggressive; favour hot open habitats; strong competitive influence
Subordinate Camponotini (<i>Camponotus</i> , <i>Polyrhachis</i>)	Co-occurring with above, submissive to them; large, often nocturnal
Hot Climate Specialists (<i>Melophorus</i> , <i>Meranoplus</i>)	Arid-adapted; specialisations that reduce interaction with Dominant Dolichoderinae
Cold Climate Specialists (<i>Prolasius</i> , <i>Notoncus</i>)	Centred on cool temperate zone; most abundant where Dominant Dolichoderinae scarce
Tropical Climate Specialists (<i>Oecophylla</i> , <i>Tetraponera</i>)	Centred on humid tropics; most abundant where Dominant Dolichoderinae scarce
Cryptic Species (<i>Solenopsis</i> , <i>Hypoponera</i>)	Predominantly within soil/litter; little interaction with epigaeic ants
Opportunists (<i>Rhytidoponera</i> , <i>Paratrechina</i>)	Unspecialised 'weedy' species; found on disturbed or low ant diversity sites
Generalised Myrmicinae (<i>Pheidole</i> , <i>Crematogaster</i>)	Cosmopolitan, found in most habitats; rapid recruitment to food
Specialist Predators (<i>Myrmecia</i> , <i>Cerapachys</i>)	Large species, small colonies; little interaction with other ants

interpretation. Within savanna systems, they found only six published studies of termite-fire interactions – four from Africa and one each from Australia and South America. Three of these considered single fires, and three (all from Africa) dealt with wider fire regimes, but each of the latter only with the contrast between annual burning and fire exclusion. Only mound-building termites were considered, and trials were not replicated. More generally, however, termites appear to be resilient to fire. For some species, this might reflect a structure whereby a single colony is composed of a number of separate 'satellite' nests, a system known as polycaly. The extent of this habit in termite assemblages is largely unknown, but Abensperg-Traum et al. (1996, for Australia) suggested that during fire some termites could migrate temporarily to the less susceptible nearby nests. In their context, harvester termites that depend on above-ground food are likely to be more susceptible to fires than are soil-feeders or within wood-feeders, whose ways of life intrinsically supply chances of refuge. The fate of the Australian *Drepanotermes tamminensis*, an obligate mound-building species, was investigated from direct dissection of 20 mounds in burned and unburned sites 3 years after a high intensity fire. Effects appeared to be severe, including a high proportion of abandoned mounds (40 % compared with 10 % in unburned areas), low numbers of termites in occupied mounds in burned areas, and higher extent of mound invasions there by predatory *Iridomyrmex* ants. These findings were believed to be consistent with the hypothesis that high floristic diversity, by providing a range of regeneration units for different foods for this polyphagous species, may enhance resilience of such harvester termites to fire.

These examples indicate the considerable difficulties in studying fire impacts on insects. The study limitations listed for Australian invertebrates (New et al. 2010) have far wider relevance and collectively indicate many of the shortcomings exemplified by examples in this book. These limitations, applying to a high proportion of studies surveyed across south eastern Australia, are (1) a major focus on ground-active taxa, using pitfall traps, mostly as the sole method of sampling; (2) relatively short duration, usually of 3 years or less; (3) opportunistic, many of them simply gathering data after a fire rather than examining critical hypotheses with before-after measurements and valid control sites; (4) a lack of pre- and post-fire data on the same study patches, including continuous data from 'control' unburned patches; (5) analysis of sampled insects only to higher taxa, such as families or orders, rather than separations to species/morphospecies levels; (6) having very incomplete background on soils, vegetation, topography and site history; (7) lacking information on fire intensity and other regime components such as area and severity of burns; (8) having been superimposed on areas with incompletely documented (or unknown) fire history, in some examples of even when the most recent previous fires occurred; and (9) lack of knowledge of extent and causes of changes in assemblage structure and susceptibility to fire.

Clarifying the impacts of fire on insect assemblages or species depends on biological understanding, and different motivations are involved in (1) fundamental studies to elucidate fire impacts and (2) need to use fire for threatened species management. In the first context, a study species or group may be selected pragmatically on criteria that furnish information and allow specific well-considered hypotheses to be addressed. Thus, Severns (2003) selected the saturniid moth *Hemileuca eglanderina* for study (p. 126) because (1) its large egg masses, used for population assessments, are conspicuous; (2) it is monophagous at the study site, facilitating definition of some critical resources; and (3) the local race he studied was restricted to the wet prairie habitat of interest, and had not been found in other nearby biotopes. In the latter context, such selection is not available, and the management undertaken is commonly much more uncertain.

In general, studies on the impacts of fires on fauna comprise three broad approaches. In conjunction, the impacts of single fires and of fire regimes may need to be distinguished carefully, with the latter needing long term studies to detect parallel long term ecological changes. The impacts of a single fire and the cumulative impacts of a regular fire regime may differ substantially. For both of these, most published studies are based simply on observations and lack experimental treatment. They commonly draw opportunistically on an unexpected single fire, or on fires designed for purposes (such as for establishment of firebreaks) other than ecological investigation, after which a limited period of inspections ensues. In addition to such observational studies, Parr and Chown (2003) also recognised 'inferred effects' (such as reduced abundance of animals attributed to loss of food supply, but commonly without quantitative justification of this) and 'experimental studies' of effects, often undertaken without adequate controls of more than very few variables influencing possible outcomes. These are the rarest form of approach.

The variety of studies is echoed, for North American prairie burn assessments, by Reed (1995, 1997) as (1) studies of a single species' response to burning; (2) comparative studies of a single fire or a series of control burns or wildfires on single burned and unburned sites; (3) long-term comparisons of burned and unburned sites; and (4) historical descriptions of pre-settlement and post-settlement prairie, as seeking to define a 'natural condition'. She added that 'Studies vary widely in their quality and thoroughness', and that they have provided many conflicting results. More broadly, the significance of understanding historical fire regimes (and other disturbances) assumes greater importance if it is presumed that these should be maintained or mimicked for the benefit of taxa that in some way have become adapted to those regimes: the 'natural disturbance model' cited widely in, for example, forestry management (p. 154). Thus, for boreal forest Carabidae, Cobb et al. (2007) noted that imposed disturbances associated with societal and economic pressures to salvage timber have included a wide array of anthropogenic intrusions. The ecological impacts of many are poorly understood, including how their impacts differ from those of more 'natural' disturbances including historical regimes to which local fauna may have become, in some way, adapted.

Each approach is represented in field studies on responses of insects, and other invertebrates, to fire. These fall into four general categories, each very broad in scope and highly variable in detail. All are exemplified in later chapters but are noted here for perspective.

Category 1. The first are 'opportunistic studies' (usually observational or inferential) in which incidence of a wildfire (as a major ecological disturbance) creates opportunity for study of subsequent events such as survival, re-colonisation and successional development. These are usually assessed by appraising diversity and assemblage composition of one or more taxonomic groups by periodic monitoring, and comparison with unburned plots or sites in the same general region and treated as 'controls'. With only rare exceptions, 'before disturbance' data on the burned area(s) are likely to be unavailable, and this lack is a concern in interpretation because of the normal high levels of heterogeneity in insect species and assemblage distributions. Many insects are distributed very patchily in the landscape, often with the reasons for this unknown. Field entomologists are keenly aware of this, and of the difficulties of interpreting such distributions across areas that superficially appear very similar. In short, many species found in the 'control samples' and absent from the burn sites may be assumed by interpreters to have been lost, but in reality may never have been present; such problems are difficult to overcome. Many such studies rely, necessarily, on rather small plots, commonly of a hectare or less. For many of these the 'edge effects' and the character of surrounding areas may have profound influences on the consequences. Use of small experimental plots imposes severe limits on interpretation, but perhaps less so for single fires than for fire regime studies. Landscape level studies of the latter necessitate much larger plots, so that valid studies can become both long term and expensive – the Kapalga experiment in

northern Australia (Andersen et al. 2003) is one of the best-documented such studies.

Category 2. With similar caveats, the second category, fundamentally experimental and dealing with manipulated burns, can be structured more logically and informatively to ensure that pretreatment information on the plots is in place. Replicated pairs of plots are sampled over a period to establish their similarity and characterise the insects or other biota present on each – perhaps by inventory study over at least a year to incorporate seasonal variations. One plot of each pair is then burned, and the other retained as a control, and the fate of the target taxa monitored to help determine the impact by evaluating change from pretreatment and parallel trends with the control plots over the same period. Both these survey categories suffer widely from inadequate monitoring periods: ideally monitoring over at least a decade or so is needed but in practice more than about 3 years is unusual. This short period commonly reflects restrictions of funding, such as the duration of a higher degree study or government grant, but the outcome is that many such impacts are interpreted only by relatively short term sampling data, rather than a time sufficient to regain or closely approach their pretreatment condition. ‘Recovery’ of insect communities after disturbance can often take many years, and immediate responses, or short term changes, can only indicate the real impacts of those.

Category 3. A third category comprises studies (mostly observational or inferential) that attempt to counter this lack of sampling endurance over many years in mosaic landscapes, by simultaneous sampling of insects on plots of different but known fire histories, most commonly differentiated by age as ‘time since fire’, so that different successional or recovery conditions within the same general area are compared as a ‘chronosequence’, and whenever possible, also incorporate unburned control areas. Single occasion sampling, at the same time, across such different regimes may be sufficient to indicate the trends that occur. Because the historical fires occurred at different times, sometimes incompletely documented, the fire regimes may differ considerably, but it is necessary to assume that a common level of impact occurred, and that the post-fire recovery time is clear as a basis for comparison.

Indeed, for most surveys in any of these first three categories of studies, knowledge of fire history is likely to be incomplete. ‘Unburned areas’, for example, usually equate to ‘not burned recently’ or ‘not burned as recently as burned areas’, or even ‘no record of recent fire’, but it may not be clear to what extent the currently present biota have been ‘shaped’ by the historical record. Hermann et al. (1999) commented, writing particularly about forest insects, ‘A large volume of literature on fire and insects relates to habitats with fire intervals of 50–200+ years’.

Category 4. The last major category moves to a stronger taxon or biotope focus, to investigate the roles and use of fire in the management of individual species, or wider taxa, or the restricted biotope that each may occupy, and may combine any aspects of approach in doing so. The balance between a fire being a severe threat or a highly beneficial management tool in conservation of threatened species

depends on understanding the interaction of an imposed fire regime with the species' biology, and the sustainability of its critical resources. That understanding, with rather different emphasis, is applied in fires for suppression of pest species, for which vulnerability rather than security is sought.

2.6 Interpreting the Outcomes

For any form of study, the two most critical features in testing any hypotheses or seeking information on insect responses to fire are (1) deciding which taxonomic groups or species to monitor and (2) standardising how these may be sampled and evaluated. In many studies a small portfolio of different groups may provide ecological complementarity, and may be selected for indicator values, comparison with other studies involving the same taxa, as of particular interest to the investigator, or simply for convenience as they are tractable in that their taxonomy and likely responses can be interpreted easily, or that they can be sampled with little additional effort. The first two of these criteria have benefit in giving many surveys relevance in wider comparative contexts. Multiple studies of nominated insect groups also help to hone informed sampling, and facilitate understanding the outcomes by improving the background biological knowledge. Sampling methods in insect surveys are very diverse (Samways et al. 2010) and also vary considerably in the costs and difficulty of sorting and processing the catches, together with gaining taxonomic identifications of the numerous specimens.

Each selection presupposes that it is not practicable to sample and analyse all insect groups present but, for any sampling programme based on passive techniques, it is likely that substantial bycatch of non-focal taxa will be accumulated; although commonly discarded, it is preferable for this to be archived responsibly for possible future use. Limitations of funds, time, and expertise impose this selection.

Many studies have attempted to reduce costs of analysis by sorting the numerous insects collected in samples and categorising them to levels above species – commonly as insect families and occasionally only to orders. Such procedures have logistic advantages in that the categories can often be differentiated rapidly, and by people with little experience and previous expertise, but can mask much ecological variety and diversity within them. Whilst such approximations are welcomed as contributing to 'rapid biodiversity assessment', their validity may need to be considered very carefully in relation to a survey's objectives. The amounts of information lost (or, rather, not gained) may create false inferences – compositional change and taxonomic turnover within assemblages or across treatments at the most informative (species) level cannot be quantified, for example. In explaining their decision to restrict analyses to order/family levels in examining fire effects, Elia et al. (2012) remarked 'Extending the analysis to the species level was outside the scope of this study, as the aim was to understand the response of insect groups (i.e. taxa) to fire rather than single species behaviour.' The idiosyncratic individual species reactions to fire (or any other disturbance) strongly endorse need

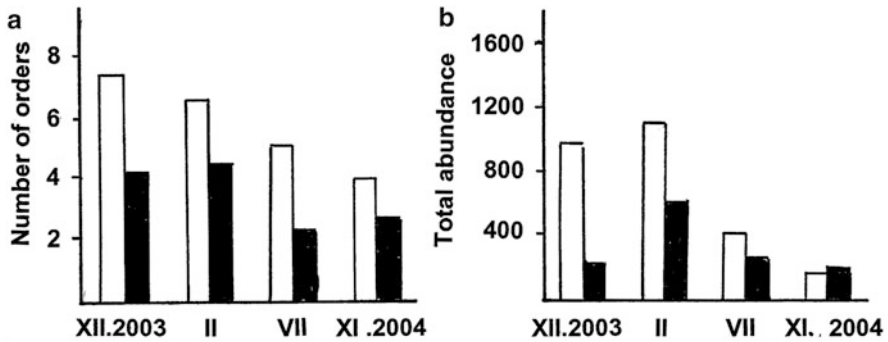


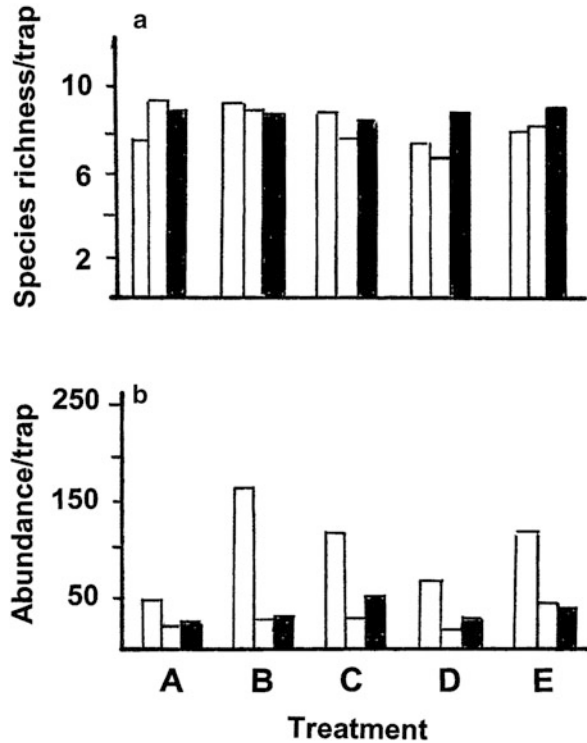
Fig. 2.7 Numbers of invertebrate orders (a) and total macroinvertebrate density (b) under burned (black) and unburned (open) miombo forest in eastern Zambia, December 2003–November 2004 (After Sileshi and Mafongoya 2006, with permission from Springer Science + Business Media)

for more taxonomically penetrating appraisal of multi-taxon samples. Most broad taxonomic groups, such as larger insect families, almost invariably contain species with very different responses to any given environmental disturbance.

However, in some studies these broad analyses can indeed be informative. Andersen and Muller (2000) showed that abundances of six (of 10 taxa) sampled by pitfall traps and seven (of 11) by sweep net samples remained largely unaffected by fire treatment in tropical northern Australia, and suggested that this demonstrated the resilience of the arthropod assemblages in relation to fire. They also noted, however, that any such inference from these data must be viewed extremely cautiously, so that ‘ordinal level analyses do not necessarily provide reliable information on arthropod biodiversity and its role in ecosystem functioning’, a sentiment agreed by many entomologists. Many, indeed, would go further and claim that such broad categories can be misleading in the simplistic trends they may imply. However, easily recognised higher categories of invertebrates have been used validly to indicate trends of abundance. For soil macroinvertebrates in the miombo forest of Zambia, population densities of Annelida, Arachnida, Chilopoda and some insect groups were lower under burned patches than unburned ones (Sileshi and Mafongoya 2006). Information such as that summarised in Fig. 2.7 indicates broad losses of soil invertebrates from burning, with some groups more sensitive than others. In that study, many of the apparent differences between burned and unburned patches were not statistically significant but impacts of fire may be inferred strongly. Larvae and pupae of Lepidoptera, for example, were absent from burned patches during the rainy season, and this absence may support the previously-advanced suggestion that forest fires adversely affect edible Lepidoptera in the region (p. 77).

Allocation of the broad taxonomic categories to trophic guild, as done by Prycke and Samways (2012) for studies of fire impacts on insects of Table Mountain, South Africa, may help to indicate resilience of key ecological roles and functions but, again, allocation at the family level may mask variety and specialisations. In

Fig. 2.8 Species richness (a) and abundance (b) of fire-favoured Coleoptera in eclector trap catches in three categories of forest stands and across five different treatments in boreal forests. Categories are clearcut (*first open*), mature managed stands (*second open*), old growth stands (*black*); treatments are A, burned; B, control; C, inoculated with *Formitopsis pinicola*; D, shaded; E, inoculated with *Resinicium bicolor* (After Johansson et al. 2007, with permission from Elsevier)



that study, trophically varied families such as Formicidae were analysed to species level. Trophic grouping has long been recognised as useful for categorising communities amongst aquatic benthic insects (p. 82), and such approaches lead to distinguishing of 'functional groups' (p. 39) that may transcend taxa and widen the values of monitoring. Some terrestrial focal groups studied elsewhere are also ecologically varied – the saproxylic beetles of Sweden, for example, were divided amongst five functional groups according to their nutritional ecology (Johansson et al. 2007), with the species favoured by fire transcending these. The treatments incorporated series of fungus-infected logs that increased guild representations, so that each 'block' of five logs comprised an untreated (control) log, a burned log, a shaded log, and two fungus-infected logs. The latter were prepared by mycelia injections of Brown rot fungus (*Formitopsis pinicola*) and White rot fungus (*Resinicium bicolor*), both key substrate conditions for many saproxylic beetles. Indeed, fungivores were the richest functional group in these trials with 114 of the 240 species included in that guild (Fig. 2.8a). Differences between feeding guilds were also evident across the treatments, but were most pronounced among wood-borers, with their generally higher richness and abundance in clearcut samples. Representation of species richness of the fire-favoured beetles, whether pyrophilous or not, in eclector traps was relatively even across a variety of boreal forest stands, but with abundance markedly greater in clearcut stands than in mature or

old-growth areas (Fig. 2.8b). The two predominant fire-favoured species (*Pityogenes chalcographus*, *Orthotomicus laricis*) are both early successional species likely to be favoured by newly created habitat, rather than by burned wood itself. In boreal forests ‘fire specialist’ beetles are ecologically varied, interpreted by Muona and Rutanen (1994) to indicate that a substantial proportion of forest beetles have become adapted to fire cycles. Many trophic groups benefitted from fire – they included a number of predatory species that live under tree bark, as well as taxa associated directly with dead or injured trees. These outcomes illustrate the complexity of beetle assemblages in different stand types, with differences across all main functional guilds and a need to conserve dead wood substrates in a variety of decay stages and stand ages in order to sustain the fauna. In this system, fire is only one influential management component, and reserves of undisturbed old growth forest are also an important resource.

As another example, Dawes-Gromadzki (2007) allocated her macroinvertebrates from a study in northern Australia to one of three trophically-based functional groups as (1) ecosystem engineers (termites, earthworms); (2) litter transformers (cockroaches); and (3) macropredators (spiders, pseudoscorpions, centipedes, ants, beetles) and recognising that this is overly simplistic but reflects categorisation of related studies in the region. That very brief study, spanning only 2 weeks before and 2 weeks after a fire, suggested that impacts were only on the third group, notably on ants.

Even very closely-related species may differ greatly in their response to fire, so that interpretation of higher group trends may be misleading. The three groups of litter arthropods surveyed in Western Australia’s Jarrah (*Eucalyptus marginata*) forest by Abbott et al. (2003), namely Blattodea (29 species), Orthoptera (74 species) and Araneae (385 species) indicated that most species were resilient to low intensity management burns conducted after logging and compared also with pre-treatment samples. However, the cockroach assemblage changed markedly after logging and in the first year after burning, but recovered almost completely after 4 years.

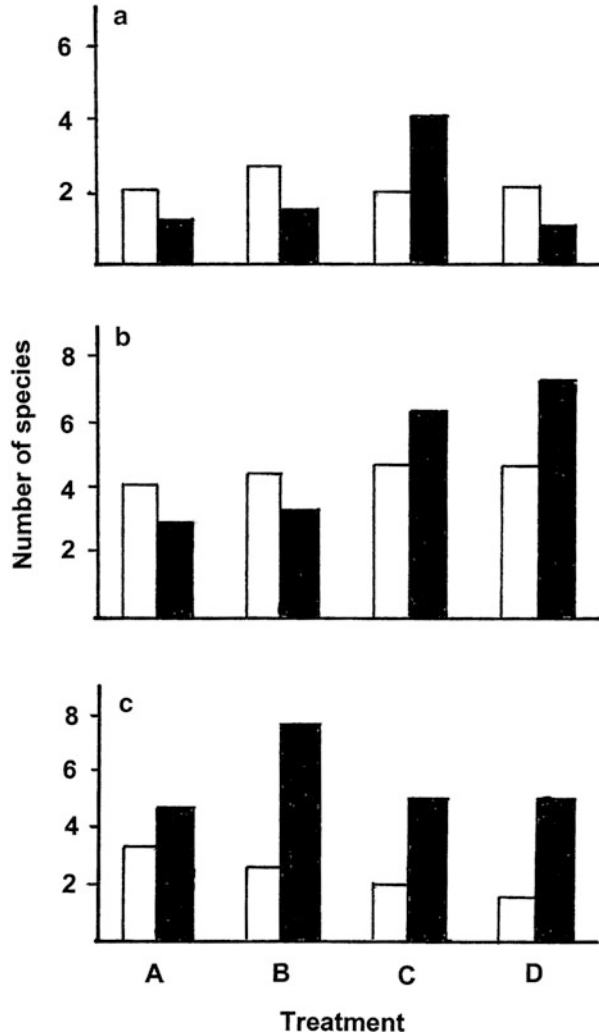
Comparison of unburned and burned heathland plots in south eastern Australia revealed some such differences in incidence – two rather similar species of *Lepidosira* (Collembola) appeared to show opposite responses to fire (Greenslade and Smith 2010). *L. nigrocephala* was found only on burned plots, and normally occurs in open vegetation communities with high ground temperatures. *L. australica* was found only on unburned plots, and is usually associated with wooded communities. Both species are widespread in the region, and have clearly different ecological needs. Such subtleties are likely to be widespread amongst arthropods, and most such differences cannot be revealed without species level interpretations: even genus level separations, as the finest level that may be acceptable to many ecologists without seeking specialist taxonomic inputs, masks such differences.

Species-level analyses are thus the ideal in any such monitoring, but are often very difficult to achieve. Even gaining consensus over what constitutes a species within any group can be difficult. The major practical dilemmas are lack of time and

funds for the detailed sorting needed, and the paucity of available taxonomic expertise to undertake identifications – with such interpretations confounded in many places by high diversity, intricacy of taxonomic characters, and presence of many undiagnosed or undescribed species so that published literature (even if available) is likely to be highly incomplete and even misleading through conveying an impression that the included taxa are indeed definitively known: such is only rarely the case, especially for regions beyond the northern temperate zones. One major limitation to considering termites in fire studies (p. 38), despite their abundance and substantial ecological roles in savanna ecosystems, is the relatively poor species-level taxonomy available. For example, De Souza et al. (2003) attempted to assess fire impacts in Brazil solely at the genus level, and found no major changes after fire. They ventured that cerrado termite genera escaped local extinctions in burned areas because (1) fires may not be sufficiently intense to kill colonies in soil or in clay-walled mounds, that thereby constitute effective refuges; (2) populations may be able to recover quickly, reflecting the large number of populations in a highly heterogeneously-burned landscape; and (3) absence of feeding specialisation and low level of interspecific competition minimise the impacts of reduced food supply.

Their 13 genera represented a level of diversity rather similar to that in the more detailed South African savanna termites study by Davies et al. (2012) with 18 genera and approximately 23 species – with some taxa acknowledged as not tractable below generic level. However, the South African taxa could be allocated amongst four ‘feeding groups’, designated to demonstrate the range of feeding substrates in the group and so in part paralleling the series of ‘functional groups’ developed to summarise aspects of ant ecology (p. 39). The termite feeding groups (Donovan et al. 2001) are (1) non-Termitidae, feeding on dead wood or grass; (2) Termitidae with varying foodstuffs including dead wood, grass and leaf litter; (3) Termitidae feeding on humus in upper organic soil layers; and (4) Termitidae that are true soil-feeders. This study covered three different savanna types along a rainfall gradient in the Kruger National Park, each with different fire regimes (annual dry season, triennial dry season, triennial wet season, unburned) compared. All termites from the two sampling methods deployed (cellulose baiting – a method that targets wood-feeding species, direct searches) were very resistant to fire impacts (Figs. 2.9 and 2.10), with little difference in response in relation to fire frequency or season. Some changes in assemblage composition and in the balance between feeding groups were probably linked with changes in vegetation structure caused by burning. The subterranean habit of many termites protects them from much direct damage from fires, as does mound-building. Comparison of termite mound densities in savanna in Ghana (Benzie 1986) showed that, in general, unburned plots had higher numbers of both harvesters and non-harvester termites than burned plots, and that the total abundance of harvesters increased after only a year free of burning, and continued to increase. The predominant species was *Trinervitermes geminatus*, and this trend reflected the decrease in dead grass and litter in burned environments and its progressive accumulation afterward.

Fig. 2.9 Species richness of termites (Isoptera) in three South African savanna areas (**a**, **b**, **c**) as recorded by cellulose baits (*open*) and active searching (*black*) under four different burning regimes as: **A**, dry annual; **B**, dry triennial; **C**, wet triennial; **D**, unburned control (After Davies et al. 2012, with permission from John Wiley & Sons)



Taxonomic difficulties evident in several of these termite studies exemplify the needs for some form of consistent differentiation in order to gain estimates of ‘species richness’. The widely used practical approximation of ‘morphospecies’, whereby samples taken during insect surveys are differentiated consistently into groups deemed equivalent to species (with, wherever possible, expert advice sought on the validity of these), is attractive in facilitating an equivalent level of interpretation and enumeration and is a practical necessity for interpretation of many taxonomic groups. As in many other contexts of analysing field samples of insects in ecological studies, consistency and quality control are vital, together with voucher specimens to enable comparison across samples and across different studies.

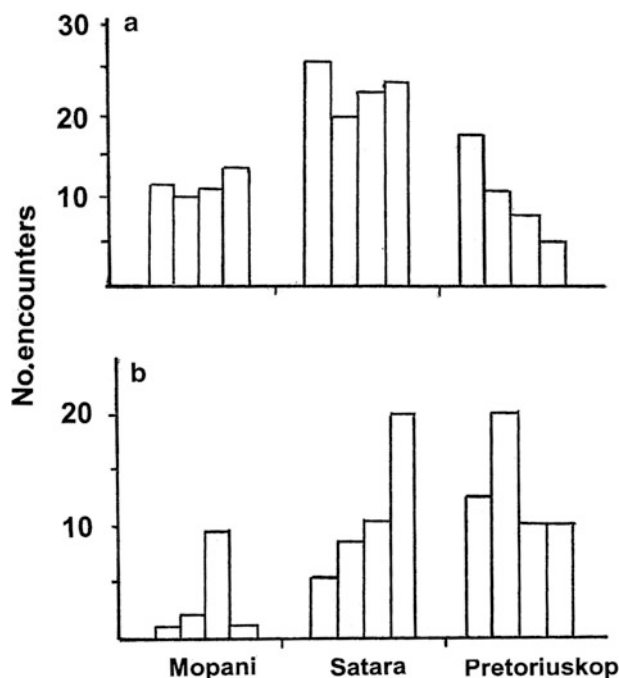


Fig. 2.10 Abundance of termites, given as numbers at cellulose baits (a) and as recorded by active searching (b) under four burning regimes across three South African savanna sites. For each block, burning treatments, from *left to right*, are dry annual, dry triennial, wet triennial, unburned control (After Davies et al. 2012, with permission from John Wiley & Sons)

A universal problem in quantitative comparisons of insects across treatments or samples is simply that many of the taxa present will be recorded only in very low numbers; very commonly species represented by single specimens are the most numerous abundance category, but the dilemma arises over whether (and how) to include these in analyses. Fire impact studies are no exception, with many published accounts reporting very low numbers of some taxa which, whilst presence contributes to 'richness' estimates, do not contribute more meaningfully to understanding changes or differences in assemblage composition. One guideline adopted widely has been to exclude low abundance species from statistical comparisons. Thus, in surveys of carabid beetles in chronosequence surveys of recovery from fire in Oregon conifer forests (Niwa and Peck 2002) and following earlier recommendation to appraise only species that comprise $>3\%$ of the total catch, only 5 of the 17 species were sufficiently abundant for analysis. Even then, the fifth-ranked species (*Zacotus mathewsii*) comprised only 3.8 % (559 of the 14,703 individuals) across the nine paired burned/unburned site comparisons. In the same survey, spiders were analysed at the more embracing family level: only 7 of the 24 families were suitable for analyses. In another North American forest example, in Canada, only 31 of the 262 beetle species/morphospecies sampled by

Saint-Germain et al. (2013) each comprised >0.5 % of the 10,348 individuals captured, and only these taxa were interpreted further.

2.7 Focal Groups

As in most other insect sampling exercises, it is usually impracticable to analyse all the numerous groups that are present. Most fire response studies, indeed, have assessed only single taxonomic groups or a small portfolio from these numerous possible candidates. This approach is expedient, and may also dictate the sampling methods and protocols to be used (Chap. 3). Broadly, the greater the number of taxonomic groups or feeding guilds appraised, the greater the sampling variety and intensity needed, and the greater the cost of the exercise. Many of the cases noted above emphasise taxonomic diversity, and the changes in assemblages of species incidence and richness. The parallel need is to sustain the full range of ecological processes that invertebrates influence and maintain, a need that leads to consideration of functions or ecological roles of those taxa. This aspect is far more difficult to study and is, as a consequence, less often evaluated.

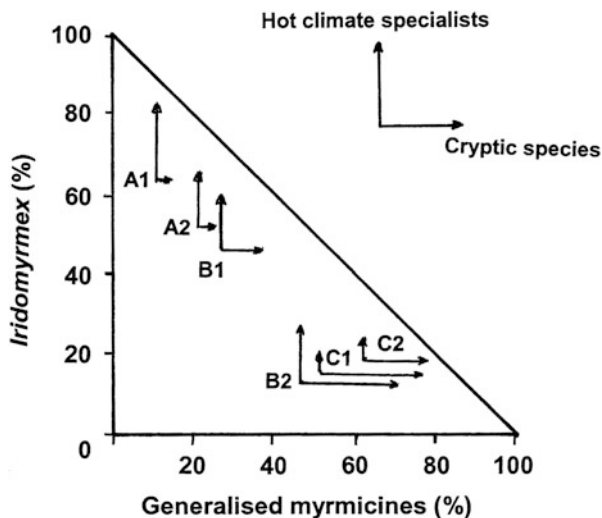
‘Development of functional classifications for animals based on life history, resource use and behaviour’ has been listed as a requirement to help assess faunal needs in assessing fire responses (Driscoll et al. 2010), whilst Moretti and Legg (2009) noted the likely parallels in traits between plants and invertebrates. Any such aids to predicting responses can markedly validate otherwise more casual surveys, and inform management.

A few insect and related arthropod groups predominate in surveys, and may be categorised by habitat as epigaeic (in soil or on/near the ground surface) or on vegetation or free flying, found mostly above the ground. Favoured epigaeic groups include Formicidae, some Coleoptera, Collembola and Araneae, whilst commonly assessed above-ground taxa include Lepidoptera (especially butterflies), Hemiptera, some Coleoptera, and Orthoptera. The predominance of these groups reflects their ecological variety and ‘accessibility’ both in terms of being sampled by relatively easy and standard methods, and the ecological and taxonomic knowledge available to interpret the samples obtained. Thus, ants were considered ideal candidates as bioindicators in Australia because (1) they are abundant and diverse in many biotopes; (2) functionally important across various trophic levels; (3) can be sampled and sorted reasonably easily; (4) have assemblage composition very sensitive to ecological changes; and (5) can be classified into meaningful functional groups (Vanderwoude et al. 1997). Each of the above-mentioned groups is sufficiently diverse and varied, and sufficiently well understood, to provide sound information on impacts and trends, as changes in species richness, absolute and relative abundance, and assemblage composition as measures of both initial impact and later recovery. In short, they have many of the features desirable in ‘monitors’ for ecological impacts and recovery, and display a variety of traits by which their responses to fire and other disturbances can be evaluated, so that changes amongst

species and wider assemblages can be interpreted sensibly. Each is also amenable to sampling by economical and easily documented approaches that can be replicated easily. Several insect groups, and spiders, are thereby recurrent foci in fire-related surveys, and examples of the traits they show are discussed throughout this book (see Chap. 7, in particular). These groups have been evaluated for their changes in many aspects of land management or site modifications; background information on their responses, and the nature, extent and duration of these both for species and assemblages is likely to be available in relation to particular imposed disturbances, of which fire is one. Measures of change include changes in species richness, overall abundance, relative abundance, and species composition of the assemblages present. However, claims for the wide values of some groups as 'indicators' may need careful investigation to determine the contexts for this. Butterflies have been mentioned as a suitable indicator for landscape-scale 'health' of ecosystems during prescribed fires over sufficiently large areas (Covington et al. 1997), but different trends may occur if contrasting single species responses with assemblage richness or composition changes. Fleishman's (2000) surveys of butterflies on burned and unburned (control) areas of central Nevada revealed that burning did not have significant effects on species richness, with community similarity (assemblage composition) changes associated with burning no greater than those found as background changes not associated with any burning treatment. Responses of butterflies to re-introduction of prescribed burns for forest land management in the western United States were assessed by transect walk counts on prescribed burn and control unburned sites (Huntzinger 2003). In both areas examined, burned sites supported considerably more species (Ashland, Oregon: 24 compared with 13 in control sites; Yosemite, California: 34 compared with 20 species). The differences were attributed to creation of open habitats not previously available and leading to increased heterogeneity and diversity of herbaceous plants. These beneficial trends were enhanced by including additional treatments in regional management, here of fuel breaks and burning riparian strips.

Amongst ground-dwelling arthropods, ants are the most frequently assessed taxon, with investigations in many parts of the world endorsing their values as indicators or monitors of ecological changes, through changes in species richness, abundance and the balance of the various 'functional groups' within local assemblages. Ants are commonly used to detect or monitor impacts of environmental changes, and the trajectories of decline or recovery. Ease of sampling by pitfall traps (below) and the likely richness and ecological variety within local faunas are often informative, in all major kinds of study on fire impacts. Short term resiliency may be apparent (p. 145), but other studies have explored the longer term consequences of fire regime impacts, particularly in savanna systems in which ants may predominate in ground fauna. In South African savannas, responses of ants to fire were linked to changes in habitat structure and cover, with differences between burned and unburned plots less pronounced in lower rainfall areas, in contrast to greater differences in higher rainfall regions (Parr et al. 2004). In northern Australia, Andersen (1991) used ants to demonstrate impacts of changes in habitat architecture, especially those flowing from fire effects on litter accumulation and

Fig. 2.11 Vector diagram to illustrate relative abundance of some major functional groups of ants in experimental fire plots in northern Australia. Treatments are: A1, A2, burned annually; B1, B2, burned biennially; C1, C2, unburned (Andersen 1991, with permission)



insolation. As well as impacts on the ants themselves, these factors influenced competitive interactions, especially amongst the dominant species of *Iridomyrmex*. In Victorian heathland, pre-fire dominant taxa (*Iridomyrmex*, *Monomorium*) were dramatically reduced after fire (Andersen and Yen 1985), with that ‘competitive release’ linked with increased abundance of several species previously considered uncommon. Andersen compared pitfall catches of ants on sites subjected to one of three different fire regimes – burned annually, burned biennially and unburned for more than 14 years – to reveal that the ant communities on the biennially burned plots were largely intermediate between those on the other treatments. Analysis of the functional groups (Table 2.3) showed the major difference between the two more extreme treatments (Fig. 2.11) with the two biennial plots rather different in their affinity, one grouping with each of the other regimes. Annually burned plots were dominated by Hot Climate Specialists and Opportunistic species, whilst the long unburned plots were characterised by high numbers of Generalised Myrmicinae and Cryptic species. Similar changes in functional group representation were reported in longleaf pine savanna in Florida (Izhaki et al. 2003), where large increases in the Dominant Dolichoderine *Forelius rugosus* (as the only member of this functional group in the pool of 30 ant species found) some months after burning apparently caused decline of some others, including Generalised Myrmicinae. Tuna-baiting every 1–3 months from before a fire until 6 months afterward revealed immediate post-fire decline of Generalised Myrmicinae far greater than for other functional groups, and that response may have been largely responsible for the overall reduction in species density and richness. In contrast, *Forelius* increased substantially after the fire. However, the fire impact was short-lived, and ant richness the following May was similar to that of the previous, prefire, May. In this example, as in others, impacts may reflect a combination of

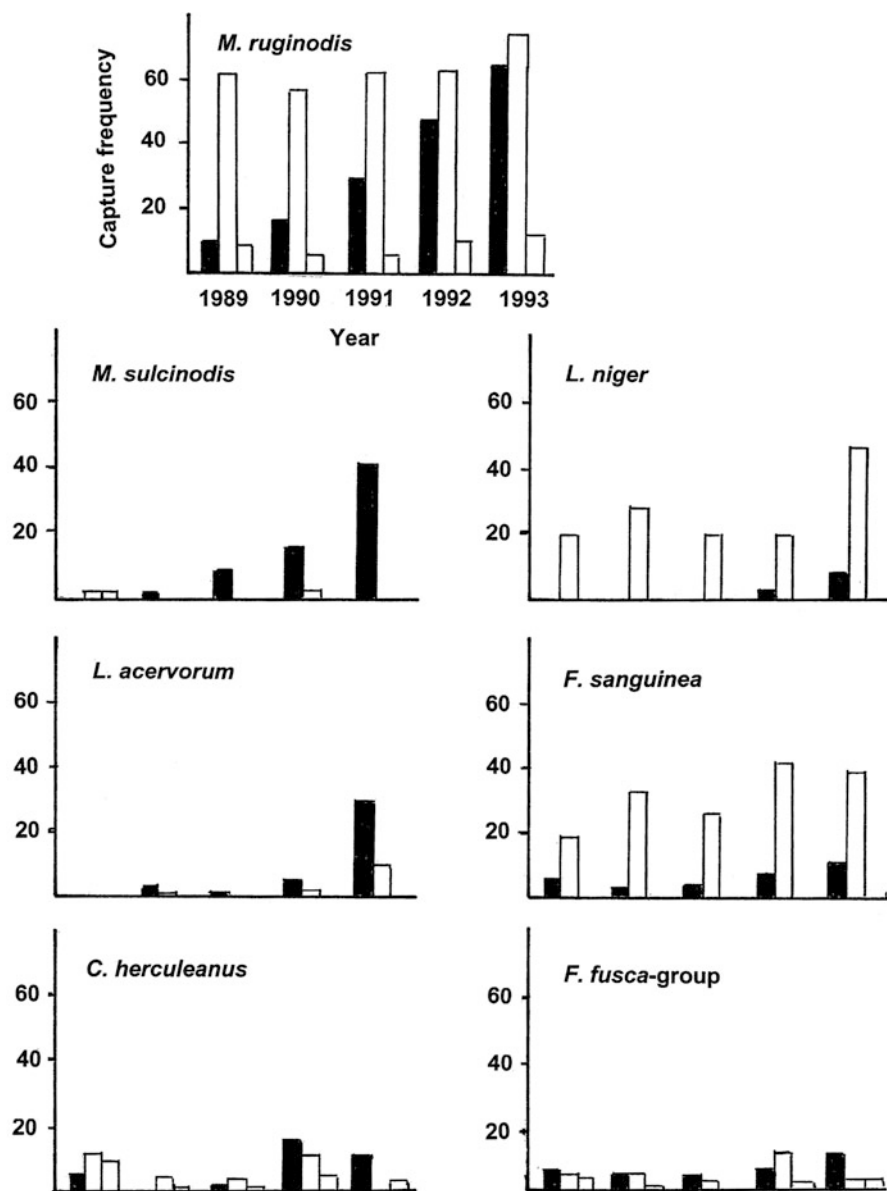


Fig. 2.12 Representation, as capture frequency, of common ant taxa in boreal forest. Treatments are: burned clearcut (*black*), unburned clearcut (*open*), mature forest control. The last has sampling effort only one quarter that in clearcut treatments (After Puntilla and Haila 1996). Taxa are: *Myrmica ruginodis*, *M. sulcinodis*, *Lasius niger*, *Leptothorax acervorum*, *Formica fusca* group, *F. sanguinea*, *Camponotus herculeanus*; notation shown for *M. ruginodis*

Table 2.4 Functional traits of ants used in study of fire impacts in Mediterranean fauna (After Arnan et al. 2013)

Trait group	Trait	Data type and states
Social structure	Colony size	Quantitative: no. workers/colony
	No. queens	Ordinal: 0 (monogyny); 0.5 (both monogyny and polygyny); 1 (polygyny)
	No. nests	Ordinal: 0 (monodomy); 0.5 (both monodomy and polydomy); 1 (polydomy)
Resource exploitation	Worker size	Quantitative: body size, mm
	Worker polymorphism	Mean worker size divided by range worker size
	Diurnality	Binary: 0 (not strictly diurnal); 1 (strictly diurnal)
	Behavioural dominance	Binary: 0 (subordinate); 1 (dominant)
	Seed-eating	Fuzzy ^a : 0–1
	Insect-eating	Fuzzy: 0–1
	Liquid food-eating	Fuzzy: 0–1
Reproduction	Ratio queen: worker size	Quantitative: mean queen size divided by mean worker size
	Colony foundation type	Ordinal: 0 (dependent colony foundation); 0.5 (both dependent and independent colony foundations); 1 (independent colony foundation)

^aFuzzy: scores range from ‘0’ for no preference to ‘1’ for high preference

loss of arthropod food resources, elimination of specialised microhabitats and impact on subsurface microclimates.

Recovery of ant assemblages after fire is also very varied. Comparison of burned and unburned clearcut areas of Finnish forests suggested that different successional processes occurred in these initially ant-free areas, and were attributable to habitat differences and possible competition between two species of *Myrmica* (Puntilla and Haila 1996). Both treatments resulted in loss of wood ants (*Formica* spp.) as the dominant taxa of old-growth forests, but the developing assemblages in burned and unburned clearcuts continued to diverge (Fig. 2.12). The burned clearcut areas were characterised by colonisation and growth of colonies of *Myrmica sulcinodis*, and steadily increased numbers of *M. ruginodis*. Unburned clearcuts, in contrast, were rapidly occupied densely by *M. ruginodis*, which apparently benefitted from the conditions of increased light and relatively high moisture. *M. sulcinodis* did not colonise these areas during the study.

For the needed appraisals of functional changes from disturbances such as fire, ants are still the most frequently-assessed insect group, drawing on the functional groups noted in Table 2.3, in some cases with functional traits compiled in rather different ways. For part of the Mediterranean ant fauna, sampled in north-east Spain, Arnan et al. (2013) used a suite of 12 ‘functional traits’ to address (1) whether fire changes ant functional composition in the community, and (2) whether any such change is due to changes in the relative abundance/dominance of species, or more to replacement of species with different traits. Different trait patterns (Table 2.4)

were found on burned and unburned plots along a series of 22 sites, and major changes in ant communities were associated with burning. In common with some other observers, Arnan et al. noted that fire destroys the nests and entire colonies of vegetation-nesting species that may become locally extinct in burned areas. Conversely, soil-nesting ants are far more likely to survive, but must then contend with a highly modified foraging environment. Across species, Arnan et al. (2013) found larger colony sizes and larger ants in burned than in unburned areas – the latter trait possibly influencing their foraging capacity. Both of the trends noted (abundance/dominance changes, replacement species) occurred, with overall species richness remaining rather similar (Arnan et al. 2006). A significant suggestion was that fire promotes higher functional diversity of ants, driven mostly by replacement rare species with unique combinations of functional traits. Those species, however, are highly susceptible to extinction, so that later disturbance could remove them and lead to rapid change (or loss) of ecosystem functions.

As might be expected from such a diverse focal group, responses of ants to fire are very varied, and some investigations have failed to detect any substantial changes (Underwood and Fisher 2006). Thus, overall ant species richness changed little during 2 years following experimental fire regimes in another study in northern Australia (Hoffmann 2003), and frequently burned sites (over 20 years) in New South Wales had similar richness to unburned sites – although this reflected replacement of species not previously present (York 2000). Whilst such turnover may be common, and undetected other than by species-level interpretations, not all ant species are susceptible to fire. *Pogonomyrmex rugosus* in New Mexico was apparently unaffected in not changing immediately after a fire or by a year afterward (Zimmer and Parmenter 1998). However the wide variety of ant biologies amongst different species and of experimental designs purported to examine changes means that ‘general conclusions are challenging to make’ (Underwood and Fisher 2006, p. 175). It follows that clear description of sampling methods and experimental designs are integral to interpreting any such studies. Likewise, information on fire intensity and history has major importance. Low severity burning (with less than half the organic layer burned, but most ground vegetation destroyed) had little impact on ant populations in Sweden (Gibb and Hjalten 2007) – possibly reflecting that both burned and control areas had previously been clearcut so had already undergone major disturbance. Many of the 16 ant species present were soil nesters, with this refuge probably an effective protection against low intensity fire (p. 38). Purported linkages of ant richness with vegetation cover following fires are very varied, and influenced also by climate. Mediterranean ant communities in drier areas recover more rapidly after fire than those living in moister areas, in which fewer species are adapted to warmer open areas. Arnan et al. (2006) thus suggested that richness of Mediterranean ant communities depends on the vegetation type present before the fire, so that recovery depends on the recovery of that vegetation. Whilst direct mortality from fire is the major immediate selective factor affecting assemblage composition, those effects are clearly different on the various species because of where (sheltered in soil or in wood or other retreats, or exposed on vegetation) and how (foraging and activity patterns affecting exposure) they live.

Removal of vegetation by fire can also raise ground temperature by increased insolation, perhaps allowing the area to be used (or avoided) by species sensitive to such change.

Epigaeic beetle studies are dominated by surveys of Carabidae, also sampled most commonly by pitfall traps or baits – and also diverse, taxonomically tractable and ecologically varied in a wide variety of terrestrial biomes. They are heralded widely as a valuable indicator group, with many species responsive to environmental changes.

As for Orthoptera (Howard and Hill 2007), different taxa of ants or beetles can be regarded as ‘fire tolerant’, ‘fire intolerant’ or ‘fire neutral’, but allocation of individual taxa to one or other group may be influenced strongly by local conditions and fire regime characteristics.

The four most intensively studied insect taxa on vegetation above ground are Orthoptera and Hemiptera (both mainly in grassland and low vegetation-dominated environments), Coleoptera (largely in wooded environments, with saproxylic taxa (p. 104) depending on dead wood a major focus in forest management: they are sometimes referred to as the insect group that suffers most from modern forest sanitation practices, as their critical resource need is actively diminished), and Lepidoptera (most environments). Amongst the last, diurnal taxa (butterflies and a few groups of moths) are the most frequently appraised, with nocturnal moths less often studied. Studies on Hemiptera are fewer than for any of the other three listed orders, and some such focal groups are far less rich than typical ant assemblages, and their suitability for investigation may vary geographically. In the Mediterranean region, where fire is one of the major disturbance agents in many ecosystems, Fattorini (2008) noted that Tenebrionidae (Coleoptera) display many of the desirable features of indicator taxa, and advocated their values in studying fire impacts on wider insect communities in local arid or semiarid biomes. Tenebrionids generally have low mobility, and are thus vulnerable to rapid losses from fire, with both soil-dwelling species (most of them flightless) and arboreal species affected. In a later study, Fattorini (2010) used pitfall traps to investigate such changes between burned and unburned plots of pine-oak forest in Italy, and also used direct hand-searching, over a year. The ten species trapped varied considerably both in abundance and their relative abundance across burned and unburned areas. The predominant species in burned areas (*Tentyria grossa*) was rare in unburned woodland and, as an open habitat species associated with dunes, its increase was attributed to changed vegetation structure (Fattorini 2010). Conversely, two species (*Accanthopus velikensis* associated with native woodland; *Colpotus strigosus* found more widely under bark and stones in woodlands) were completely absent from burned areas.

For all of these groups, most studies have addressed only the relatively mobile and recognisable adult stages. Despite the abundance of immature stages, their incorporation into surveys at species level is still largely impracticable for most holometabolous insect groups. However, larvae are commonly both more sedentary and ecologically restricted so that studies on, for example, caterpillars (with Lepidoptera the only large insect order for which larval forms are, at least in part,

Table 2.5 Caterpillar incidence and richness on *Byrsonima coccolobifolia* in three sites in the Cerrado Ecological Reserve, Brazil (From Diniz et al. 2011)

Number of	Areas			
	A	B	C	Total
Plants examined	900	900	900	2,700
Plants with caterpillars	202	85	39	326
Caterpillars	321	94	65	480
Species	36	24	14	49

	Months after fire in burned areas									
	2	3	4	5	6	7	8	9	10	Total
A	25	27	15	9	11	35	35	28	17	22.4
B	15	9	7	5	10	8	17	3	11	9.4
C	3	4	6	2	3	13	5	2	1	13.3

Sampled areas are (A) unburned; (B) middle dry season fires; (C) late dry season fires. Upper part of table indicates overall outcome of sampling, as numbers; lower part of table gives percentage of plants with caterpillars during each of 9 months of collection (December–August; May–August [7–10] is the ‘dry season’)

accessible for study) may provide valuable additional insights to surveys of adult stages alone. One such survey, of the Lepidoptera larvae associated with *Byrsonima coccolobifolia* (Malpighiaceae, an abundant shrub/small tree in Brazilian cerrado) assessed caterpillars from burned and unburned trees by direct examination of 900 plants in each of three treatments (Diniz et al. 2011) at monthly intervals for 9 months (Table 2.5). Although numbers were rather low (480 caterpillars across 49 species in 16 families), greatest abundance was in the unburned area. However, only eight species were found in all three treatments, and 34 species were ‘rare’ as represented by fewer than five individuals. Some species apparently exploited flush growth for oviposition within a few months of fire.

Each of the insect groups emphasised above, and a range of studies on others, demonstrates the complexity of responses to fire, with those responses influenced by local circumstances and generalisation restricted by lack of knowledge of individual taxon tolerances and biology, and of the richness and functional structures of assemblages and wider communities. Intelligent use of fires in conservation management demands capability to predict outcomes based on biological understanding which, for most insects remains elusive and difficult to integrate intelligently with other management needs. Additional studies of impacts and of the subsequent trajectories of recovery (p. 35) are crucial in improving this situation.



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