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The Use of Glyphosate Herbicides in Managed Forest Ecosystems and Their Effects on Non-Target Organisms with Particular Reference to Ants as Bioindicators

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INTRODUCTION

This publication reviews and synthesizes the results of many research studies designed to elucidate the ecological effects of the herbicide glyphosate used in forested landscapes. We have not intended our review to be an exhaustive review of all published studies (both laboratory and field investigations) concerned with faunal and floral glyphosate interactions and the environmental fate of glyphosate. We particularly focused on studies that had relevance to north temperate forest ecosystems and selected published investigations to incorporate into our review that cover a wide range of faunal and floral taxa that might be exposed to herbicides during applications.

This review was initiated as part of a research project conducted by Drs. Woods, Drummond, and Stubbs, at the University of Maine, to elucidate the effects of the use of glyphosate on insect communities associated with the Maine forested landscape. Our field research focused primarily on the Hymenoptera (ants, bees, and wasps). Ants are one of the dominant groups of animals (with several taxa considered keystone species) associated with forested landscapes in North America, and they are associated with many important ecosystem processes such as soil nitrogen cycling, soil aeration, predation, and seed dispersal (Hölldobler and Wilson 1990). Therefore, we incorporated into this general review of the impacts of glyphosate on resident fauna and flora the potential role that ants might play as bioindicators, that is, as measures of ecosystem disturbance, particularly of the effects of herbicide use in forested landscapes.

Herbicide Use in Forested Landscapes

The application of herbicides to clearcut timber and pulp production land is a common forest management practice (Miller and Wigley 2004). They have been used for more than 60 years in managing vegetation in North American temperate forests (Wagner et al. 2004). Herbicides such as picloram, 2,4-D, glyphosate, hexazinone, imazapyr, triclopyr, sulfometuron methyl, and metsulfuron methyl are sprayed to selectively remove or kill non-economic trees and shrubs, which often compete with timber or pulp species for light, water, space, and nutrients (Steward et al. 1984; Sweeney et al. 2002; Shepard et al. 2004). Wagner et al. (2004) present a review of herbicide chemical classes used during the past 50 years in forest management. Herbicide application encourages early regeneration and rapid growth of the desired species of crop trees (Newton et al.

1992; Freedman et al. 1993; Lautenschlager 1993; Pitt et al. 1993; Sullivan et al. 1998; Shepard et al. 2004). In addition, herbicides are used in forested landscapes to manipulate wildlife habitat and for management of invasive plant species (Shepard et al. 2004).

Herbicide use in forest timber and pulpwood management falls into three categories (Shepard et al. 2004): site preparation (after harvest and before planting to minimize competition from non-crop shrub and tree species); release treatments (herbicides applied two to four years after planting or harvest to remove competing hardwood non-crop trees that compete with crop conifer species); and herbaceous weed control (herbicides applied three to four months after planting to reduce herbaceous weed competition with the seedling crop trees). Estimates of the percentages of total herbicide usage in the United States and Canada are significant: 28% to 44% is for site preparation, 27% to 29% for release tactics, and 29% to 43% are for herbaceous weed control (Shepard et al. 2004). It is difficult to estimate the total amount of acreage and herbicide active ingredient applied across forest landscapes, but a review of statistics (USDA Forest Service data) by Shepard et al. (2004) suggest that approximately 74,450 ha were treated with 46,075 kg of active ingredient in the U.S.A. during 2002.

Maine Forest Ecosystems

In Maine, red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) are economically important trees that are common and represent the dominant components of late-succession forests. Both species require relatively cool, moist conditions to germinate and become established (Blum 1990; Frank 1990). These species are very shade tolerant and will survive for many years in an understory of a mature forest with as little as 10% ambient light. This may not be true in young forest stands under shrubs and hardwoods. However, these valuable economic tree species also respond to full sunlight with accelerated growth rates (Blum 1990; Frank 1990). Rapid growth and the attributes of the wood produced make these species (particularly spruce) valuable for pulp production. Cyclic outbreaks of the spruce budworm (*Choristoneura fumiferana*) have historically synchronized stand development into two even-aged cohorts, a dominant overstory cohort and a younger cohort that becomes established in the understory (Kucerall and Orr 1981; Seymour 1992). Under natural conditions, mortality of mature trees by the spruce budworm leads to the release of this younger cohort, which then becomes the dominant age class.

The even-aged nature of spruce-fir forests and economic considerations have led to the use of clearcutting in Maine as a common method of harvesting (Seymour 1992). With adequate, undamaged regeneration in the understory, the harvest will result in the release of the younger cohort and re-establishment of a spruce-fir canopy. However, in mixed hardwood/softwood stands, or in stands with inadequate regeneration in the understory, clearcutting can result in the establishment of hardwood species that can out-compete the slower-growing softwoods. This is particularly true in stands where hardwoods regenerate from stump sprouts and benefit from the established root systems and energy reserves. The use of herbicides becomes useful in re-establishing softwoods when there is a moderate density of established softwoods that would benefit from reduced competition from the hardwood species (early release). Typically, one application is adequate to allow the softwoods to become dominant and shade out any intolerant hardwood species (Wagner 2000; Shepard et al. 2004). While herbicides in Maine forest landscapes are primarily used in conifer release, other uses are also common (Daggett 2003; Wagner et al. 2003; and see below).

Benefits vs Costs of Herbicide Use

Many studies have shown that the use of herbicides in the management of North American forests increases commercial forest productivity (Miller and Miller 2004; Wagner et al. 2004). The magnitude of increased production varies from 10% to 450% across all forested regions of North America (Miller and Miller 2004). Therefore, there is a significant economic incentive to include herbicides in the suite of forest-management tactics. Several scientists have concluded that when an herbicide is used at recommended rates, under optimal environmental conditions, it poses minimal toxicological hazards for terrestrial vertebrates or risk of bioaccumulation (Morrison and Meslow 1983; Atkinson 1985; Lautenschlager and Sullivan 2002; Tatum 2004). As herbicide applications have become more common, interest in the short- and long-term indirect effects of herbicides on non-crop vegetation and concerns for effects on non-target animals have been raised (Freedman 1991; Miller and Wigley 2004). These concerns, in part, have been the impetus for a large number of studies addressing both direct and indirect effects of herbicides used for forest management. Sullivan and Sullivan (1993) compiled a list of 402 references on the effects of glyphosate on non-target organisms from a total of 2500 found with a computerized literature search. There are even more published studies that have appeared since the early 1990s (Sullivan and Sullivan 2003) and as stated in the

introduction this review, we have taken a selective sample of the voluminous published studies that exist at present.

While the toxicity of most herbicides to animals is remarkably low (Atkinson 1985; Tatum 2004), the current controversy concerning the effects of herbicides applied in forest management on non-target species relates mostly to the indirect effects of herbicide applications. An example of an indirect effect of herbicide applications is the resulting reduction of the abundance and richness of floral resources that serve as needed energy sources for most species of insects. Therefore, a reduction in the abundance and diversity of plants might result in a concomitant reduction in the invertebrate fauna (Dajoz 2000).

Invertebrates play many important roles in forest ecosystems, including nutrient cycling, herbivory, fungivory, pollination, and predation, so the potential effect of forest-management practices, especially herbicide applications, on forest ecosystems may be dramatic. Approximately half of all described organisms are insects and 50% of insect species diversity is comprised of herbivores (Daley et al. 1998). Insect herbivores influence ecosystems by consuming a variety of plant tissues, which can affect primary production, restrict the geographic range of plants, and influence nutrient availability by leaching nutrients from damaged plant surfaces (Schowalter 2000). Insect herbivores may augment the diversity of plant species both during insect outbreaks and when insect damage enhances the penetration of sunlight sufficiently to increase the reproductive success of other plant species (Price 1997; Carson and Root 2000; Hartley and Jones 2003). Pollinators increase the spread and help maintain the fitness of host-plant populations, so the conservation of pollinator communities is central to plant biodiversity in most ecosystems (LaSalle and Gauld 1993; Kearns and Inouye 1997; Stubbs and Drummond 2001). Pollinators rely on the floral community for both adult flight energy resources and larval food (Bugg et al. 1989; Jervis et al. 1993). As predators and parasitoids, insects can relieve stress placed on vegetation by regulating population densities of insect herbivores. Insects, including dragonflies, true bugs, beetles, lacewings, ants, wasps and flower flies, are important predators in most terrestrial ecosystems (Messina and Sorenson 2001, Michaud and Belliure 2001; Wang and Tsai 2001; Griffin and Yeargan 2002; Hentz and Nuessly 2002).

Nutrient cycling is a key process in forest ecosystems that is performed by insects and other soilborne arthropods. Ants, termites, springtails, mites, sowbugs, beetles, and flies are some of the most abundant arthropods involved in nutrient cycling (Daly et

al. 1998). In addition, many other more cryptic invertebrates such as nematodes, earthworms, slugs, and snails, and microorganisms such as protozoa, bacteria, and micro-fungi are also important in the turnover of nutrients (Freckman 1988; Coleman 2004). Most nutrient cycling occurs in the topmost horizons of the soil (Ingham et al. 1985). The decomposition of organic matter recycles nutrients back into the soil. In general, arthropods, annelid worms, and mollusks break down larger pieces of organic matter into smaller pieces that can then be decomposed more efficiently by microorganisms (Simmons 1982).

Ants (Formicidae) are one of the most abundant predators of arthropod herbivores, detritivores, parasites, and other predators in forest ecosystems. It is currently estimated that ants constitute a high proportion of the biomass of many landscapes, making them the predominant predator in most ecosystems. For example, it has been estimated that one-third of the animal biomass of the Amazon rain forest is composed of ants and termites. When considered with bees and wasps, ants and termites make up more than 75% of the total insect biomass on earth (Hölldobler and Wilson 1990). The presence of ants in the forest may influence herbivory, pollination of flowering plants, seed dispersal, and nutrient dynamics in the soil and thus indirectly affect the abundance and diversity of vegetation (Culver and Beattie 1983).

Non-crop Forest Vegetation

Many investigations have focused on the short-term effects of glyphosate and other herbicides used on forest vegetation. It is usually the deciduous shrub and tree species that are targeted for herbicide application in site-preparation and release-management tactics (Shepard et al. 2004). Herbicides such as glyphosate can reduce non-crop plant cover and diversity in the short-term, although recovery of the non-crop plant community begins in the first two to three years after application (May et al. 1982; Santillo et al. 1989a; MacKinnon and Freedman 1993; Bell and Newmaster 2002) with no differences between treated and non-treated stands observed five years after treatment.

Though the recovery of non-crop vegetation may begin in the second year following treatment, some recovery may not occur until the fourth year following treatment (MacKinnon and Freedman 1993). Non-crop plant species are usually not eliminated from herbicide-treated sites (Freedman et al. 1993; Miller and Miller 2004), but a change in the abundance or a retardation of growth rate of non-crop plant species occurs and is evident in the increased pres-

ence and success of conifers. This retardation of growth, compared to increase in plant mortality, has been found to be true in most studies that look at the effects of herbicides on forest vegetation (Freedman et al. 1993; Freedman 1995; Lautenschlager 1990; May et al. 1982; Morrison and Meslow 1983; Newton et al. 1992; Santillo et al. 1989b; Thompson and DeGraff 2001; Miller and Miller 2004). Several studies have addressed the question of the richness and diversity of non-crop plant species following herbicide application. Though there may be some immediate effects of herbicide treatment on plant richness and diversity (usually detrimental), in at least in one study, there was no reduction of indigenous seed-producing plant species after five years (Bell and Newmaster 2002). In another study comparing manual cutting of stump sprouts and cut-stump applications of glyphosate in a young mixed plantation, the species richness, diversity, structural diversity, and turnover of herbaceous plant, shrub, and tree communities were not significantly different (Lindgren and Sullivan 2001). Therefore, herbicide applications may have the same effect as manual cutting even though the latter might be less selective. In considering the role of several vegetation-management treatments on the diversity of cryptogams (ferns and other non-flowering plants), Newmaster et al. (1998) found that herbicide applications had more of an impact on the species diversity and abundance of cryptogams than mechanical clearing or clearcutting) In a follow-up study, Newmaster and Bell (2002) found some recovery five years after treatment. In many cases, the mechanisms for these impacts have not been elucidated. On bottomland forest sites previously used for agriculture, sites treated with glyphosate had increased broad-leaved herbaceous plant cover three years after treatment compared to non-treated sites, but grass biomass and species diversity were not affected after the second year (Groninger et al. 2004). In two other research studies, the richness of moss species was reduced soon after glyphosate treatment, but only for the first two years after treatment (Lautenschlager and Sullivan 2002; Bell and Newmaster 1998).

In general, release treatments (usually single herbicide applications), do not reduce the richness or diversity of herbaceous plant species (Miller and Miller 2004), but instead alter the succession trajectories of plants (Guynn et al. 2004). In a review of the short-term impacts of herbicides on non-crop vascular plants, 12 studies reported that species richness and species diversity either were not affected or were increased, while only one study reported a decrease in the diversity of shrub species (Sullivan and Sullivan 2003). In southern U.S. forests, however, the diversity of

herbaceous plant species can be suppressed for up to 15 years when herbicides are applied consecutively for three to five years (Miller and Miller 2004). Contradictory results have indicated there can be a short-term increase in herbaceous vegetative cover as a result of glyphosate application under a release treatment (Freedman et al. 1993). This increase in herbaceous plant cover can be dramatic and also is important as bird habitat. Welch et al. (2004) and Jones and Chamberlain (2004) discuss the benefits of using herbicides in conjunction with prescribed burning for providing early-successional habitat for northern bobwhite in southern U.S. pine plantations.

The long-term impacts of herbicide application on forest vegetation are predominately associated with differences in softwood and the species composition of non-crop hardwoods and shrubs. Newton et al. (1992) observed long-term effects on tree height of shrubs and hardwoods and vegetation cover of seven-year-old clearcuts sprayed with triclopyamine, glyphosate, or 2,4,5-T. In this study, the leaf area of hardwoods and shrubs was reduced by at least 50% for up to two years after treatment. Differences in height and the percentage of cover remained for at least nine years after herbicide treatment, with conifers growing faster than the non-crop deciduous tree species on herbicide-treated sites. In a study by Miller et al. (1999), species richness or species diversity of non-crop woody and herbaceous vegetation did not differ 11 years after treatment with the following herbicides: hexazinone liquid, hexazinone pellets, glyphosate, triclopyr, picloram, and a mixture of dicamba or 2,4-dichlorophenoxyaetic acid. However, Miller et al. (1999) found the proportion of pines relative to hardwoods was greater and shrub density was higher in herbicide-treated sites. In boreal forests treated with broadcast applications of glyphosate, Boateng et al. (2000) found, an increased species richness of the herbaceous community and reduced dominance of the tall shrub community for 10 years following the application of the herbicide. In plots that were spot-sprayed, however, they found no differences in the structure of the plant community (Boateng et al. 2000).

Therefore, in the short-term the abundance or biomass of non-crop deciduous trees and herbaceous vegetation, the species diversity, and the species richness sometimes can be reduced by herbicide applications, but recovery begins within the first two to four years after treatment. In the long-term, species of woody and herbaceous plants are generally not eliminated, though differences in height, percentage of cover, and stand density of non-crop herbaceous, deciduous, and coniferous plants remain.

Non-Target Fauna—Birds

Concern over the effects of glyphosate on non-target animals has led to a wide range of research including studies on the effects of glyphosate on birds, small and large mammals, fish, amphibians, multicellular invertebrates, and unicellular microorganisms (Sullivan and Sullivan 1993). Herbicides appear to be mostly non-toxic to birds (Batt et al. 1980; Latka 1992; Lautenschlager and Sullivan 2004), but there are examples of slightly toxic direct effects (Hoffman and Albers 1984). For the most part, it is hypothesized that any deleterious effects from herbicides would be indirect effects on birds' forage or nesting habitat since the response of early-successional songbirds to a shortened period of suitable habitat may reduce populations (Freemark et al. 1995; Lautenschlager and Sullivan 2004). However, the results reported in the literature are variable and suggest that herbicides have little indirect effect on the abundance of forest-dwelling bird species, but may have transient effects on compositions of bird communities.

Kilgo et al. (2000) reported on the results of several studies on the effects of herbicides used in site preparation for pine plantations on birds. In one study, the diversity of bird species was higher in herbicide-treated sites compared to non-treated sites in the second and third years following treatment. No differences were apparent by the fifth year after treatment in this study. However, Kilgo et al. (2000) concluded that, based upon most other studies, bird diversity and richness did not differ between herbicide-treated and non-treated southern U.S. pine plantations.

In a release-treatment study, songbirds, including common yellowthroats (*Geothlypis trichas*), Lincoln's sparrows (*Melospiza lincolnii*), ruby-throated hummingbirds (*Archilochus colubris*), and palm warblers (*Dendroica palmarum*), colonized non-sprayed plots earlier than sprayed plots (Santillo et al. 1989a). The authors attributed this to a temporal change in plant succession following glyphosate application because clearcuts were sprayed several years after the bird census. In another study, songbird abundance was lower in black spruce (*Picea mariana*) plantations two and three years after herbicide and manual-release treatments (thinning by cutting) (de Bellefeuille et al. 2001b). In an evaluation of nesting habitat preferences for the warbling vireo (*Vireo gilvus*), dusky flycatcher (*Empidonax oberholseri*), Swainson's thrush (*Catharus ustulatus*), American robin (*Turdus migratorius*), and chipping sparrow (*Spizella passerina*) after manual thinning plus an herbicide application in conifer plantations, Easton and Martin (2002)

determined that deciduous regrowth did not occur during the three years after treatment in the herbicide-treated plantations and that birds preferred nesting sites with a high component of deciduous vegetation. Birds used patches of non-treated vegetation or selected alternative species of trees in which they normally would not nest (Easton and Martin 2002). Although the number of bird species decreased, the total abundance of birds increased, and common bird species became numerically dominant, almost to the exclusion of other species (Easton and Martin 1998). Lautenschlager (1993) reviewed eight studies concerning the effect of herbicide treatments on northern songbird populations and found total songbird populations were rarely reduced after the first year following treatment. Three out of seven studies documented a decline in densities of some songbirds associated with brushy vegetation habitat for at least the first year following herbicide treatment (Sullivan and Sullivan 2003). Thus, indirect effects on bird populations of herbicide application appear to be short-term and associated with the composition of the vegetation in the study site. Lautenschlager and Sullivan (2004), however, point out that quantifying the effects on bird populations at a landscape level is fraught with problems. They emphasize that one must be careful when interpreting the results of many of the studies that have been conducted.

Non-Target Fauna—Small Mammals

Studies in both southern and northern U.S. coniferous ecosystems suggest that herbicide treatments may suppress populations of small mammals in the short term, but that populations recover quickly. Atkeson and Johnson (1979) showed that populations of small mammals initially were reduced by herbicide application followed by a prescribed burn, but after 18 months there were no differences in the abundance of small mammals between either the treated or non-treated southern pine sites. The abundance of some small mammal populations also decreased following glyphosate application in northern conifer forests (Santillo et al. 1989b), though there may not be any changes in the diversity of small mammals at the community level (Sullivan et al. 1998). Herbivores (Microtinae: voles, lemmings, and muskrats) were less abundant in treated plots for the first two years following application, while insectivores (Soricidae: shrews) were less abundant for at least the first three years following treatment (Sullivan et al. 1998). In another study cited by Sullivan et al. (1998), there was no difference in the abundance of omnivores (Cricetinae: hamsters; Zapodidae: jumping mice)

between the herbicide-treated and the non-treated control plots; however, there were fewer red-backed voles (*Clethrionomys gapperi* (Vigors)) in the herbicide-treated sites for two growing seasons after the treatment. This decline was attributed to a reduction in vegetation cover as documented by de Bellefeuille et al. (2001b), Gagne et al. (1999), and Miller and Miller (2004). Alternatively, there were no detectable effects on the abundance of populations of deer mice (*Peromyscus maniculatus* Wagner), yellow-pine chipmunks (*Tamias amoenus*), red-backed voles and long-tailed voles (*Microtus longicaudus* Mernam) (Runciman and Sullivan 1996). Snowshoe hares (*Lepus americanus* Erxleben) avoided recently clearcut areas regardless of whether the area was treated with herbicides or was manually released because of the general lack of protective cover (de Bellefeuille et al. 2001a). The mountain hare (*Lepus timidus*) avoided herbicide-treated sites for one year (Hjeljord et al. 1998). Some studies, however, have shown temporary increases in small mammal populations following herbicide application (Anthony and Morrison 1985).

So what do the majority of studies tell us? Lautenschlager (1993) reviewed 14 studies relating to the effect of herbicide treatments on small mammals and found that small mammals responded to herbicide treatments in species-specific ways. Some small mammals were not affected by herbicide applications. Some species preferred herbicide-treated sites, while others avoided herbicide-treated sites. Results demonstrated that transient individuals or visitors to the plots (immigrants) were reluctant to choose disturbed sites (herbicide treated), while residents of previously disturbed sites were not affected by an additional form of disturbance. Another extensive literature review of 12 studies, revealed that none of the authors reported significant decreases in the richness or diversity of small mammal species (Sullivan and Sullivan 2003). The researchers all suggested that short-term decreases in populations of small mammals were related to changes in habitat due to the herbicide treatment (an indirect effect), rather than to a direct toxic effect. Although the dynamics of microhabitats in forest stands including stumps and leaf litter have large effects on populations and capture rates of small mammals (Dueser and Shugart 1978, Planz and Kirkland 1992), the literature does not appear to support the likelihood of direct toxic effects of herbicides used in forest management on mammal populations (Wahlgren 1979; Brewster et al. 1991; Freedman 1991; Tatum 2004).

Non-Target Fauna—Large Mammals

We have found no literature that suggested there is a direct toxic effect from herbicides on large mammals, which indicates that the herbicide application in forest stands will affect large mammals (mostly deer and moose considered) through the availability of food (Guynn et al. 2004; Lautenschlager and Sullivan 2004). However, there are only a few documented cases that found differences in the amount of browse for large mammals after herbicide applications.

Keyser et al. (2003) applied herbicide in forest clearcuts and measured the response of the plant community for three consecutive years. Although cover and species richness of non-crop herbaceous plants declined during the first year after herbicide application, no additional differences were observed during the last two years of the study. Eschholz et al. (1996) studied the short- and long-term effects of glyphosate applications on the use of clearcut stands for browse by moose (*Alces alces*) in Maine. In the short-term (one to two years following treatment), moose tracks were less abundant on treated sites, but over the long-term (seven to 11 years after treatment) they were more abundant on treated sites. The authors theorized that this was because increased conifer density in the long-term increased habitat for bedding and foraging. In this same study, herbicide treatment reduced browse (deciduous shrubs and tree saplings) during the first and second years after treatment, but after seven to 11 years there was more browse in the treated sites and moose fed more heavily in those sites (Raymond et al. 1996). In considering the effects of glyphosate on summer forage for deer in Maine, Vreeland et al. (1998) found that the biomass of deciduous leaves was greater in untreated sites one year after treatment, but seven to 10 years after treatment the differences were not significant. In a study conducted by Sullivan et al. (2002) in the western U.S.A., moose showed no preference in their use of conventionally or chemically thinned lodgepole pine. However, the authors also found that mule deer (*Odocoileus hemionus*) used conventionally thinned plots more than unthinned plots. When comparing forest regeneration methods, Bergquist et al. (2003) found that browse damage by roe deer (*Capreolus capreolus* L.) on spruce seedlings (*Picea abies* L. Karst) was more frequent in sites treated with herbicides, but among herbicide-free treatments, mechanically scarified plots were most heavily browsed.

Looking at southern U.S. pine plantations, Miller and Miller (2004) summarize the impact of herbicide applications on large mammals. They suggested that in some regions of the South her-

bicide applications may reduce the availability of browse favored by white-tailed deer compared to a non-treated control for the first year. By the second year, however, there was no difference in the level of browse in the treated and non-treated plots. In other areas where southern pine is managed, deer browse may actually be enhanced by herbicide application because it suppresses undesirable woody vegetation that deer do not use, allowing release of preferred browse.

In a review of 14 studies, Lautenschlager (1993) summarized much of the available information on the effects of herbicide application on moose and deer. The results of these studies indicated browse could be reduced for up to four growing seasons following treatment. The use of treated sites by moose and deer generally remained unchanged or even increased during the first growing season after treatment, but after eight years browse was three to seven times more abundant in herbicide-treated sites (depending upon herbicide chemistry, formulation, and rate). The short-term effects of herbicide application on browse and cover may indirectly reduce populations of moose and deer, but in the long-term, treated sites may have more available browse and bedding (Sullivan and Sullivan 2003). It appears that there are few if any significant long-term deleterious effects on large mammals due to forest herbicide applications (Lautenschlager and Sullivan 2004).

Non-Target Fauna—Fish and Amphibians

Less research has been conducted on the direct and indirect effects of forest herbicide applications on aquatic vertebrates (Thompson et al. 1991; Kreutzweiser et al. 1994; Guynn et al. 2004). Bioassays of the direct toxicity of herbicides suggest that glyphosate herbicides used at recommended rates pose little or no risk of acute toxicity to salmonids (Chapman 1989; Holtby and Baillie 1989; Morgan et al. 1989; Janz et al. 1991), trout (Folmar 1976; Hildebrand et al. 1982; Morgan and Kiceniuk 1992), and flagfish (Holdway and Dixon 1988). However, at higher concentrations (exceeding recommended rates) some herbicides have acute toxic effects on fish (Folmar et al. 1979; Feei 1987; Mitchell et al. 1987; Holdway and Dixon 1988; Wan et al. 1988; Morgan et al. 1989) and can cause changes in behavior (Morgan et al. 1991; Morgan and Kiceniuk 1992). Triclopyr oil-soluble ester formulations have been found to be highly toxic to salmonids, whereas amine formulations have been found to be non-toxic to salmonid species. This suggests that in addition to the specific active ingredient, the formulation can be important in determining deleterious effects on fish (Kreutzweiser

et al. 1995). Some trout can detect herbicides in the water, which elicits an avoidance reaction (Morgan et al. 1991). These laboratory studies are difficult to translate into estimates of the lethal effects of herbicides to fish in surface waters, so field studies may better estimate these risks to fish populations.

Some studies have monitored the response of fish populations in natural bodies of water following herbicide application. Two are reviewed here. The short-term effects of glyphosate spray on rivers inhabited by Coho salmon (*Oncorhynchus kisutch*) indicate a smaller catch per unit effort up to two weeks following treatment (Reynolds et al. 1993). Morgan and Kiceniuk (1992) studied the short-term impacts of aerial spray drift into rivers inhabited by rainbow trout (*Oncorhynchus mykiss*). They found no effect from a two-month exposure of herbicide in these surface waters.

Amphibians are the dominant vertebrate species in north temperate forest ecosystems (Burton and Likens 1975; Merritt 1987; Duguay and Wood 2002). Salamanders are found in higher densities in old-growth forests because regenerating timber stands have more light penetration and lower relative humidity, which creates a more stressful environment for amphibians than old-growth forests (Pough et al. 1987; Duguay and Wood 2002). Therefore, it might be expected that herbicide treatment of regenerating stands could produce an environment stressful to amphibians. Cole et al. (1997) researched the short-term effects of glyphosate on capture rates of amphibians in Oregon clearcuts. They found no difference in the capture rates of lungless salamanders or Ensatinas (*Ensatina eschscholtzii*), Pacific giant salamanders (*Dicamptodon tenebrosus*), or western redback salamanders (*Plethodon vehiculum*) from habitats treated with different herbicide application regimes. However, Relyea (2005), in a test conducted in cattle tanks containing approximately 1000 L of water and no sediment, found that glyphosate resulted in high mortality of some amphibian species. They observed approximately 100% mortality for tadpoles of the following amphibian species: leopard frog (*Rana pipiens*), gray tree frog (*Hyla versicolor*), and the wood frog (*Rana sylvatica*). The Roundup® brand formulation at the tested concentration did not have significant effects on the American toad (*Bufo americanus*), the spring peeper (*Pseudacris crucifer*), or the spotted salamander (*Ambystoma maculatum*). Relyea's (2005) conclusions, however, have been controversial because cattle tanks may not adequately simulate a stream or pond ecosystem.

We conclude from this review of the literature that applications of herbicides in forests do not have deleterious effects on aquatic

or semi-aquatic vertebrates. However, there have not been enough studies under field conditions to allow us to suggest that the opposite is true (Lautenschlager and Sullivan 2004).

Non-Target Fauna—Invertebrates

Because of the small number of field studies that have been conducted to date, the effects of glyphosate use on forest invertebrates is poorly understood (Guynn et al. 2004). In general, invertebrates are usually underrepresented in environmental impact studies. The direct toxicity of herbicides to invertebrates appears, in general, to be quite low (Folmar et al. 1979; Gardner and Grue 1996; Simenstad et al. 1996; Peterson and Hulting 2004; Bohan et al. 2005). Thus, as with the vertebrates, we might expect that the indirect effect of glyphosate herbicides on non-crop plant diversity and abundance may be the mechanism for any observed effects on invertebrates.

Soil microorganisms

Conclusions from studies on the effects of glyphosate herbicides on soil microorganisms have been quite variable, ranging from stimulatory growth effects in laboratory cultures (Gomez et al. 1989; Wardle and Parkinson 1990) to field studies that report the conflicting results of transient reductions in fungal activity, no effect at all (Wardle and Parkinson 1991), or stimulatory effects on population growth (Grossbard 1985, Rueppel et al. 1977). Preston and Trofymow (1989) found no direct toxic effects of glyphosate on soil microbes as measured through respiration rates. Gomez and Sagardoy (1985) and Gomez et al. (1989) found glyphosate had no effect on the density of aerobic bacteria in sandy soils. A study by Busse et al. (2001) showed glyphosate application had little to no direct effect on soil microbial communities in ponderosa pine plantations. Any effects from glyphosate are expected to vary with the species of microorganism, the type of soil, and the competitive interactions that occur between different species (Wardle and Parkinson 1992). Our review of the published studies on microbial communities in soils contaminated with glyphosate herbicides suggests that these herbicides have little or no effect on soilborne microbial communities. In other words, we think any effects of glyphosate herbicides on microbial communities are ephemeral due to the potential rapid rate of population increase (short generation time) of microbes.

Nematoda and Annelida

Almost no data have been collected on the response of anne-
lids to applications of glyphosate herbicides in forest ecosystems.
When the worm *Eisenisa fetida* was exposed to the recommended
glyphosate application rate, the worms avoided treated areas and
moved toward unexposed soil or the soil surface, but there was no
increased mortality (Verrell and Van Buskirk 2004). There have
been several studies on the response of nematodes to glyphosate
herbicides (Saly and Ragala 1984; Patra and Ray 1987; Vainio and
Hokkanen 1990; Saly 1991). While one study (Saly 1991) found
increased densities of free-living soil nematodes following applica-
tions of Roundup®, another study (Patra and Ray 1987) found this
herbicide had no effect on two species of plant-pathogenic nematodes.
The authors of these studies concluded that glyphosate herbicides
affect nematode communities through the indirect effects on plant
abundance, richness, and diversity.

Aquatic flora and invertebrate fauna

A number of studies have examined the effects of herbicides
on aquatic algae, plankton, and macro-arthropods. Austin et al.
(1991) observed that glyphosate increased the growth rate of algal
biomass in artificial stream troughs compared to the non-treated
controls. The authors speculated that the phosphorus in the her-
bicide acted as a nutrient for periphyton growth. However, Golds-
borough and Brown (1987) found that glyphosate had no effect on
periphyton communities or carbon fixation in study ponds treated
with herbicides at levels simulating a typical forest application. A
year later, however, they found a reduced rate of photosynthesis
in treated ponds. Hernando et al. (1989) found similar results in
the laboratory with *Chlorella pyrenoidosa* that had been exposed
to high levels of glyphosate. They found that glyphosate inhibited
electron transport in algae, thereby inhibiting chlorophyll synthesis
and leading to reduced rates of photosynthesis. Another laboratory
study showed that glyphosate inhibited growth of cyanobacteria at
levels of 100 ppm (Hutber et al. 1979). Compared to several other
herbicides, glyphosate has been shown to be the least toxic to green
algal, *Euglena* spp., and cyanobacteria species (Richardson et al.
1979; Maule and Wright 1984; Shindo et al. 1986). Holtby (1989)
and Holtby and Baillie (1989) showed a glyphosate application
had a direct toxic effect on stream periphyton communities under
field conditions, but they also reported that enhancement of algal
communities occurred a year after treatment. In another stream

study, Sullivan et al. (1981) concluded that glyphosate applied at the recommended rate of 2.2 kg ai/ha (Roundup®) had no effect on the abundance of phytoplankton. The majority of stream studies that evaluate the impact of field rates of herbicide appear to corroborate the conclusion that aquatic algae are not affected by treatment, or if they are, the effect is short-lived, perhaps lasting a year (Lautenschlager and Sullivan 2004). Evidence from laboratory studies, however, indicates that high levels of many herbicides can have deleterious effects on the physiological processes and growth rates of green algae, although it is questionable whether some of these laboratory studies reflect conditions of exposure that would occur under field conditions.

Laboratory bioassays with glyphosate and other herbicides have been conducted on a variety of aquatic immature insects, mostly Diptera and Ephemeroptera (Folmar 1978; Hartman and Martin 1985; Holck and Meek 1987; Buhl and Faerber 1989; Henry 1992). These studies showed that the herbicides had little or no effect on mortality except occasionally at extremely high doses. There have also been several field studies conducted to assess the herbicides' impact on benthic invertebrates. A number of studies have found little or no direct effect on aquatic arthropods when glyphosate was applied to surface waters to control undesirable aquatic vegetation (Solberg and Higgins 1993; Gardner and Grue 1996; Simenstad et al. 1996). According to Kreutzweiser et al. (1989) an aerial application of glyphosate caused no major disturbances in biomass, abundance, or species richness in stream macro-invertebrate populations. Simenstad et al. (1996) observed that the application of glyphosate to mudflats to control the wetlands plant *Spartina alterniflora* had no short or long-term effects on the benthic microfauna community. Whether studies in aquatic systems (with herbicide doses high enough to control aquatic plants) relate directly to forest ecosystems is debatable, but it is likely that at least some proportion of herbicide applications used to enhance conifer regeneration might end up in aquatic ecosystems either by drift of herbicides off the targeted site or because small bodies of surface water occur within treated forested sites (Gluns 1989; Carlson and Fiore 1993; Miller et al. 2002; Wofford et al. 2003). While it may be intended for terrestrial use, there is overwhelming evidence that glyphosate enters aquatic habitats, typically through inadvertent (or unavoidable) aerial overspray (Newton et al. 1984; Goldsborough and Brown 1989; Feng et al. 1990; Thompson et al. 2004). However, the herbicides that might contaminate non-target sites would be expected to occur in much lower doses than the rates applied to targeted vegetation (Tatum 2004).

Arthropoda

The direct effects of glyphosate herbicides on terrestrial arthropods also are poorly understood, but are suspected to be negligible (Eijsackers 1985; Sullivan and Sullivan 2003). It is estimated that less than 1.5% of all research conducted on the effects of pesticides on arthropods are represented by studies specifically investigating herbicides (Theiling and Croft 1988; Croft 1990). Assays of the direct toxicity of glyphosate on most of the arthropod species tested to date have concluded that the compound is "almost non-toxic" or "slightly toxic" (Monsanto 1982; Atkinson 1985). However, some studies have documented high mortality when arthropods were treated topically with glyphosate. For example, Hislop and Prokopy (1981) observed 100% mortality in predatory mites collected from apple orchards and treated in the laboratory. Eijsackers (1985) reported reduced longevity in springtails, isopods, and ground beetles exposed to glyphosate in the laboratory.

Field studies of the effects of herbicides on terrestrial arthropods have resulted in taxon-specific responses. The abundance of micro-arthropods, especially mites, increased in herbicide-treated sites compared to non-treated sites, but diversity and richness did not appear to be affected (Hendrix and Parmelee 1985). Similar results have been observed for spiders (Asteraki et al. 1992). Duchesne et al. (1999) found that glyphosate had no effect on total catch of ground beetles in clearcuts seven to nine years after treatment, though species richness and species diversity were higher in glyphosate-treated sites.

Most studies documenting the effects of herbicides on herbivorous arthropods have focused on direct toxic effects or sub-lethal effects, such as physiological and behavioral modification (Croft 1990). However, it is suspected that arthropods exposed to herbicides experience indirect effects (Guynn et al. 2004). Populations of insect herbivores have exhibited diverse responses to herbicide applications as a review of the following studies suggests.

Nowak et al. (2003), in a study in loblolly pine stands, found that the pupal weight of the insect pest Nantucket pine tip moth (*Rhyacionia frustrana* (Comstock)) was significantly lower and population fluctuations were more variable in herbicide-treated sites compared to non-treated sites. Population densities of parasitoids of the Nantucket pine tip moth including *Lixophaga mediocris* Aldrich, *Eurytoma pini* Bugbee, and *Hyssopus rhyacioniae* Gahan were similar on treated and non-treated sites (McCravy and Berisford 2001) indicating that these natural enemies experienced no direct effect from the herbicide treatment. This supports the authors' hy-

pothesis that the effects of herbicide treatment on the growth and development of Nantucket pine tip moth is a direct effect. Nowak et al. (2003) suggest that the significantly greater growth rates of loblolly in herbicide-treated sites may have played a role in the reduction in the moth's rate of growth and development.

Homoptera (aphids, leafhoppers, scale insects) are common insect herbivores in both coniferous and deciduous temperate forests (Baker 1972). They feed on either phloem or xylem. It might be expected that any indirect effects of herbicide treatment that alters the nutritional quality of tree and shrub species could be important to these insects since they are sensitive to changes in the quality of the host plant (Dempster and McLean 1998). The literature, however, documents only a few studies on the effects of herbicide treatment on forest-inhabiting Homoptera. In these few cases, homopteran densities were lower in herbicide-treated plots compared with brush-saw-treated plots and non-treated control plots (Ward et al. 1998; Lautenschlager and Sullivan 2002).

A study by Santillo et al. (1989a) on herbicide treatments in managed forest plots showed a decrease in the number of arthropods captured in treated sites one and three years after treatment. The authors could not attribute the decreased abundance of insect populations in the glyphosate-treated plots to densities of insectivorous mammals in these sites since mammal densities also declined over the first three years of the study in the treated sites relative to the non-treated sites. This decrease in arthropods in glyphosate-treated sites suggests that the herbicide had either a direct toxic effect on the arthropods or an indirect effect through a change in the non-crop plant community.

The indirect effects of herbicides on communities of herbivorous arthropods, in most cases, are hypothesized to be a result of reduced floral resources and the effect that this reduction would have on arthropods that require them during at least one phase of their life cycle. Flowering plants are essential resources for adult wasps (Cowan and Waldbauer 1984; van Emden 1990; Altieri 1994) and larval and adult bees (Westrich 1996; Banaszak 1996; Stubbs and Drummond 2001). Many studies have documented that herbicides have indirect effects on beneficial wasp and bees. These studies present correlative relationships that suggest that decreases in flowering plants in agricultural fields results in decreases in the abundance of wasps and bees and often concomitant increases in the density of insect pests (Pimentel 1961 Adams and Drew 1965; Dempster 1969; Flaherty 1969; Smith 1969; Root 1973; Altieri et al. 1977; Altieri and Todd 1981; Risch 1981; Altieri and Letourneau

1984; Andow and Risch 1985; Andow 1991): see Barbosa (1998) for a review of this topic. This phenomenon, increased populations of natural enemies as a response to increased floral resources, is the basis for the recently emerging field of conservation biological control (Barbosa 1998).

Summary of Non-target Effects

In general, the application of glyphosate in forest landscapes to suppress the growth of non-crop deciduous shrubs and trees appears to have limited immediate direct effects on non-target fauna. Long-term negative effects of glyphosate also appear to be limited in scope, although some species are affected. These long-term effects on the animals are most likely caused indirectly by the altered plant community and levels of light penetration. Some of the documented effects of the use of herbicides for site preparation or release are contrary to any hypothesized negative effect of the herbicide on resident fauna. In fact some studies have shown that the density of non-target species increases in herbicide-treated clearcuts relative to non-treated clearcuts (Hendrix and Parmelee 1985; Santillo et al. 1989a; Asteraki et al. 1992).

The cause of contradictory findings, however, has not been convincingly demonstrated. Several explanations are plausible, but highly speculative. One possible explanation is that the use of herbicides may open up a habitat by reducing overall vegetative cover, thus enabling insectivorous predators to find prey more easily and resulting in a numerical response (increased immigration of predators) into the habitat (Santillo et al. 1989a). A second possible explanation is that the reduction of vegetative cover following the use of herbicides may also reduce the amount of shade, which would provide more exposed ground surface and create a warmer micro-climate favored by some species of ants (Hölldobler and Wilson 1990). A third possibility is that the reduction of the diversity of flowering plants creates an environment that makes it easier for specialist herbivorous insects to detect host plants. A theory to explain an increase in herbivores in monoculture agroecosystems is the resource concentration hypothesis (Root 1973). This hypothesis suggests that increased plant diversity makes it more difficult for specialist herbivores to find and to colonize their host plants. It has also been suggested that the use of glyphosate herbicides maintains communities of forest plants in early successional states for a longer period of time than in untreated sites. Thus, there are more flowering plants for longer periods of time in treated sites. We might then expect to find in these sites an increase

in the abundance and diversity of those invertebrates that depend upon flowering plants (bees, wasps, moths, butterflies, flower associated beetles and flies).

Ants (Formicidae) are one of the dominant taxonomic groups associated with forested landscapes. As residents of forest ecosystems, ants are significant both in terms of biomass and ecosystem function. The effects of glyphosate on the structure and dynamics of their communities have not been reported. Because ants are sensitive to disturbance and are considered good bioindicators of ecosystem change, we can hypothesize that they would be affected by the use of glyphosate as a forest management tool. Lough (2003) in a two-year study found that ants were more abundant in sites that were clearcut 10 to 15 years before sampling than in sites that were clearcut three to five years before sampling. In both recent and older clearcuts, ants were more abundant in herbicide-treated sites than in non-treated sites. In this study soil pH, soil organic matter, soil moisture, hardwood density, and floral density did not explain the differences in the abundance or species diversity of ants relative to herbicide effects. However, the density of softwood stems was positively correlated with the abundance of ants in both years, which suggests that herbicide applications have an indirect effect on the ant community. At present we have no evidence of a mechanism that might result in greater abundance and diversity of ants in herbicide-treated plots, but the research does suggest that forest management practices affects the structure of ant communities in western Maine.

The remainder of this bulletin addresses the role of ants in forest ecosystems, specific aspects of their biology likely to be affected by herbicide induced environmental change, and their potential use as bioindicators of chemical disturbance.

THE IMPORTANCE OF ANTS IN FOREST ECOSYSTEMS AND THEIR POTENTIAL AS BIOINDICATORS

As discussed in the previous section, when it comes to measuring an ecosystem's response to the application glyphosate, the number of possible effects and the complexity of the responses are overwhelming. This complexity is not unique to glyphosate applications and it has led many scientists and government regulators to look at insects as bioindicators of the level of disturbance and disruption to the ecosystem's function. Measuring by abundance, biomass, and diversity, ants are one of the dominant organisms in most forested landscapes, possibly equaled only by springtails (Collembola) in abundance and biomass (Gullan and Cranston 2000). Thus, a central question might be posed: can ants be of use in assessing ecosystem-level disturbance due to anthropogenic forces such as application of glyphosate in forests? In order to explore this in a meaningful way, we first present a summary of the general biology and ecology of ants.

Predatory Behavior of Ants

In the family Formicidae, there are 11 subfamilies, 297 genera, and approximately 8,800 species currently identified worldwide (Hölldobler and Wilson 1990), and in Maine, 62 ant species are known to occur (Drummond unpublished data). Ants are major predators in forested ecosystems in Maine and throughout the world. Abiotic factors and human management may influence ant communities and in turn, may influence the performance of ants as predators. Ants prey on insect herbivores, parasites, and other predators (Hölldobler and Wilson 1990). A look at specific examples from the literature will elucidate the role of ants as predators in forest ecosystems.

In deciduous forests in Connecticut the larvae of tethered gypsy moths (*Lymantria dispar* L.) were preyed on more often by ants than by any other invertebrate (Weseloh 1989). Young gypsy moth larvae were found in higher abundance in plots where ants were not suppressed compared to plots that were manipulated to suppress ant populations (Weseloh 1993). Additionally, Sudd and Lodhi (1981) found that ant species-rich pine plantations were correlated with lower abundance of Araneae, Coleoptera, Collembola, Arthropleona, Myriapoda, and larval Diptera. Young and Campbell (1984) detected a number of ant species, including *Formica podzolica*

Francoeur, *Formica neorufibarbis* Emery, other *Formica* spp., and *Camponotus* spp., preying on pupae of the western spruce budworm in the coniferous trees utilized by ants for foraging. In contrast, Sanders and Pang (1992) determined that *Camponotus* spp. were not major predators of spruce budworm in boreal forests.

The predatory behavior of ants may benefit non-prey invertebrates. The presence of ants increased the survival of the gall-making wasp *Disholcaspis edura* Weld on *Quercus turbinella* Green in the face of parasitism by *Platygaster* sp. (Fernandes et al. 1999). In willows, generalist predatory ants preyed indiscriminately on leaf- and petiole-gall-making insects (insects that exit galls in late summer), while stem-gall-makers (insects that remain within galls to overwinter) were not affected by predation (Woodman and Price 1992). Predatory behavior by ants may be beneficial to vegetation on which ants reside or hunt. On sapodilla trees with many ants, the predatory activities of *Dolichoderus thoracicus* Smith resulted in less damage by the fruit borer *Alophia* sp. with many ants (Van Mele and Cuc 2001). Wood ants (*Formica* spp.) prey on insects that defoliate birch trees and suck the trees' sap. On trees where ants were not excluded, the autumnal moth was reduced by 45% to 67% and the birch aphid was reduced by 77% in comparison with trees on which ants were excluded. These populations of insect herbivores were negatively correlated with the number of ants. Karhu (1998) found the percentage of leaf area damaged by moth larvae was 34% lower in trees on which ants foraged. Ants use the plants for shelter and/or food and in return protect the plants from parasites and herbivores (Kleinfeldt 1978; Hölldobler and Wilson 1990; Oliveira 1997).

Other Roles Ants Play in the Forest Ecosystem

Ants as prey

In addition to being predators in the forest, forest ants also serve as prey for vertebrate wildlife (Hölldobler and Wilson 1990). Ants are the primary prey of pileated woodpeckers and flickers (Torgersen and Bull 1995). Bull et al. (1992) determined that *Camponotus* spp. and *Formica* spp. constituted 97% of the woodpeckers diet. Bears are also known to prey on ant species. Insects including *Camponotus* spp., *Formica* spp., *Lasius* sp., *Tapinoma* sp., *Aphaenogaster* sp., and yellow jackets constituted approximately 24% of the diet of black bears in Oregon (Bull et al. 2001), and grizzly bears consumed ants in years when high-quality food was scarce (Mattson 2001).

Ants as soil modifiers

Nesting and foraging activities by ants alter soil characteristics around their nests, which may affect the abundance and diversity of nearby vegetation. The composition of plant species has been correlated to the presence and size of anthills of *Camponotus punctulatus* in disturbed agricultural sites (Folgarait et al. 2002). Beattie and Culver (1977) examined the influence ants have on the alteration of their vegetative microhabitat. They observed that certain plant species were often found in proximity to ant mounds. In areas close to ant mounds, the ants had altered the soil through subterranean excavation and deposition of wastes to form midden piles (refuse piles created and used by ants). These activities increased the nutrient content of the soil and allowed plants to flourish (Beattie and Culver 1977). In temperate deciduous forests, Kristiansen and Amelung (2001) observed that the soils under abandoned anthills were enriched with organic matter, although the ratio of carbon to nitrogen and the soil pH were not affected. They found that, although the quality of the organic matter decreased over time, the changes in the soil quality were detectable for up to 20 years after the mounds were abandoned. Lenoir et al. (2001) observed that the nests of *Formica rufa* were always drier, had a higher C/N ratio, and often had higher NH_4 (+) than the surrounding forest. Lobry de Bruyn (1999) reviewed current research concerning the relationships between ants and soil and found ants may significantly influence water movement, nutrient cycling, and soil movement on a landscape scale.

Ants as pollinators and dispersal agents of plant propagules

Ants can act as pollinators (Puterbaugh 1998; Gomez 2000; Schurch et al. 2000), but their role as pollinators may depend on their relative abundance with respect to other pollinators. Ant pollination is most evident when ants outnumber other floral visitors (Gomez et al. 1996). In general, ants are only significant pollinators of a few species of plants. Flowering plants that display the "ant-pollination syndrome" grow in hot and dry habitats, are morphologically accessible to the flightless ant workers, have small pollen volumes, and have few ovules per flower, thus requiring fewer pollen transfers (Hickman 1974; Hölldobler and Wilson 1990). Gomez (2000) found ants were as effective as winged insects in the pollination of sweet alyssum, *Lobularia maritima* (Brassicaceae). Garcia et al. (1995) studied the importance of ants as pollinators of *Borderea pyrenaica* (Dioscoreaceae). This species is endemic to the Pyrenees region of the northeastern Iberian Peninsula. Their results indicated that

ants were more effective pollinators than lady beetles (Coccinellidae: Coleoptera) and Diptera, even though they were less abundant.

Ants have been well studied as dispersers of plant reproductive propagules, especially seeds (Hölldobler and Wilson 1990; Zhang et al. 1997). Some species of plants have co-evolved a mutualism with ants to enhance seed dispersal (Hölldobler and Wilson 1990). These plants are characterized by seeds with special appendages or "elaiosomes." These ant-attractive food resources are rich in fats, oils, starch, sugars, vitamins, and proteins (Beattie 1985). Ants carry the seeds back to the nest where the elaiosomes are eaten by workers and larvae. This phenomenon, referred to as myrme-cochory, occurs wherever ants are found, but is most common in north temperate forest ecosystems, in perennials in Australian and southern African dry heath and sclerophyll forests (Beattie 1983; Hölldobler and Wilson 1990). Ants disperse the seeds of many of the spring-blooming wildflowers in the forest understory in the eastern U.S.A. (Beattie and Lyons 1975a; Beattie and Culver 1981). In deciduous forests in New York, 25% of the herbaceous flowering plants are myrmecochores (Handel et al. 1981), and in some regions of Scandinavia 40% of the herbaceous plants are myrmecochores (Sernander 1906 cited in Hölldobler and Wilson 1990). In general, the size of the ant affects the distance that seeds are dispersed by ants (Ness et al. 2004). This has implications for plant reproduc-tion, particularly if small-sized ants invade a geographic region (Ness 2004). Ants can also disperse other reproductive propagules such as lichen soredia. Stubbs (1992) found that the common forest myrmicine *Myrmica detritinodis* disperses soredia of a variety of lichen species in Maine forests.

Ants, however, do not only disperse seeds, but they also feed upon them (Zhang et al. 1997). The predation of seeds by ants can alter or shape plant communities when ants consume seeds of dif-ferent species differentially (Inouye et al. 1980; Risch and Carroll 1986). Ant species that feed on seeds are found worldwide, but the highest diversity of granivorous ant species is found in grassland and semi-desert and desert ecosystems (Beattie and Lyons 1975b; Hölldobler and Wilson 1990). Other interactions between ants and plants include ants acting to defend plants, plants acting as shelter for ants (myrmecophily), plants feeding ants (extrafloral nectarines and Beltian food bodies), ants feeding plants through soil enrichment (myrmecotrophy), and ants pruning plants. Some of these interactions are beneficial to both the ants and the plants and some are neutral or detrimental to one or the other (Hölldobler and Wilson 1990).

Abiotic and Biotic Factors that Influence Ant Activities

Vegetation

In forests, ants use vegetation as foraging and nesting sites (Wilson and Hölldobler 1990). As discussed in the previous section, ants commonly forage for prey within woody vegetation. For example, ants use the canopies of fruit trees to forage for insect prey that consists of both insects that are beneficial to the trees (James et al. 1999) and insects that are pests (Paulson and Akre 1992; Rieux et al. 1999). Weseloh (2000) studied the ant *Formica neogagates* and its forage plants in northeastern U.S. deciduous forests and found that up to 150 ants can use a tree at one time and some ants will forage for up to 4 hours.

The structural diversity of vegetation may affect the availability of ants' nesting and foraging sites, insolation of the ground, and food supply so that the balance of ant functional groups changes with the predominant vegetation, land use, and disturbance (New 2000). Herbers (1989) found limited availability of nest sites and microhabitat, including soil and vegetation differences, influenced the spacing and species diversity of northern temperate ants. The diversity of ants in forests increases as vegetation mass increases, except in areas of dense, long grass (Greenslade and Greenslade 1977). Twigs from a diverse array of tree species in forests attracted 80% more species of twig-nesting ants than a collection of twigs from one species of tree did (Armbrecht et al. 2004). Deslippe and Savolainen (1994) compared the differences in the densities of *Formica* spp. nests and in the reproductive output of colonies for forest edge, intermediately grazed meadow, and overgrazed meadow habitats. The forest edge had the highest nest density and reproductive output while the overgrazed meadow had the lowest. The density of ant nests and the reproductive output of intermediately grazed meadows fell in between the levels in the forest edge and overgrazed meadow. They also noted that alate (winged reproductives) production was higher in the forest edge (Deslippe and Savolainen 1994). Tschinkel and Hess (1999) studied the ant community in longleaf and slash pine forests and found a relationship between the identity and abundance of ants and the mean tree diameter, which suggests that ant communities change as trees grow. The total number of species was similar in all tree sizes, but the identity of those species was different. Torgersen and Bull (1992) made similar observation with the use of downed woody debris by ants. They found that *Camponotus* sp. preferred large-diameter logs, though other ant species did not demonstrate a preference.

Temperature, soil characteristics, and other factors

Environmental factors, including temperature, soil moisture, soil type, latitude, and elevation, have been found to affect ants' spatial distribution and the density of ant colonies. Soil properties including percentage of clay, percentage of organic matter, available water capacity, and pH influence the distribution of ants on mixed grass rangelands, resulting in an aggregated spatial dispersion (Catangui et al. 1996). Negative correlations were found between the elevation and/or moisture of soils and the abundance, species diversity, and species richness of ants (Wang et al. 2001). Lynch et al. (1988) found that the seasonal differences in abundance and diversity of soil and litter ants were mostly independent of soil moisture, but significantly correlated with seasonal ground surface temperatures. Temperature changes had a greater effect on ant foraging activity early in the season. Soil moisture was correlated to ant abundance and species richness on a daily basis, but mean soil moisture levels were not correlated with ant abundance and richness across the season. The abundance of six of seven species of ants (including *Crematogaster punctulata, Lasius neoniger, Monomorium minimum,* and *Pheidole dentata*) was positively correlated with average ambient temperature on a monthly time scale (Albrecht and Gotelli 1999). In cooler environments, such as higher latitudes, ant broods were found only in areas of direct solar radiation. The availability of these areas may limit the availability of nest sites since shaded nest sites are excluded (Bernstein and Gobbel 1979). Weseloh (1995) studied several variables including temperature, basal area of trees in wet sites, latitude, and soil moisture and their effects on ant communities in Connecticut forests. The abundance of ants decreased with latitude and soil moisture. The number of ants observed foraging on the ground was positively correlated with temperature, but the number found in bait traps and on leaves was not. A simulation model using activity responses driven by soil temperature was a good predictor of the foraging behavior of the observed colony (Crist and Williams 1999). Latitude was the most important predictor of the density of ant species in forests and bogs of New England, though densities in forests were also strongly associated with elevation, light availability, and vegetation composition (Gotelli and Ellison 2002).

Forest-Management Practices and Ant Communities

Mechanical forest-management activities

Researchers investigating the effects of forest management have documented a variety of responses by resident ant communities. It appears that the responses of ant communities not only are specific to the type of disturbance, but also are affected by the geographic locale and the specific structure of the forest stand. Punttila et al. (1991) compared new clearcuts (zero to two years old), old clearcuts (10 years old), and mature stands (120 years old) in Finland to consider the effect of clearcutting on the composition of the ant community. They concluded that clearcuts reduced the abundance of ants compared to mature stands. However, they also noted that species richness was higher in old clearcuts than in new clearcuts or mature stands (Punttila et al. 1991). Alternatively, Lough (2003) found very few ant species in mature stands compared to young or older clearcuts in Maine.

Jennings et al. (1986) studied the impact of clearcut strips on ant abundance and diversity in comparison with residual strips and dense mature spruce stands in different age stands in northern Maine forests. The two-year study did not yield entirely consistent results, but general patterns in the abundance of ants and in the structure of their communities were evident. In the first year there were more ant species and greater ant abundance in the mature stands than in the non-cut residual or clearcut strips. The second year showed no difference between clearcuts and dense stands, but higher ant abundance and more ant species in clearcuts than in non-cut residual plots. The age of the clearcuts (one to six years) had no effect on mean ant catches or on the number of ant species captured.

Floren and Linsenmair (2001) compared ant communities in regenerating forests five, 15, and 40 years after clearcutting to ant communities in uncut mature forest stands in Malaysia. Ants were more abundant than other insects in the uncut forest. There were no differences in the proportions of ants and other insects in the five-year-old regenerated forest. As the age of the regenerated stand increased, insect diversity increasingly resembled that of the uncut forest (an increasingly higher proportion of ant species relative to other insects) and ant communities increased in structural complexity. However, this trend apparently is not universal, as Whitford and Gentry (1981) found the highest diversity and richness of ant species in longleaf pine plantations in recently replanted plantations, not in mature, thinned, or burned plantations. When

comparing Amazon forests selectively logged four and 10 years before sampling for ants, species richness, evenness, and mean abundance did not vary between treatments. The population density of many species changed, however, and species commonly found in sites that were directly disturbed by logging were rare in undisturbed sites (Vasconcelos et al. 2000). In a study in Japan, Maeto and Sato (2004) found that overall species richness of ant communities was not different, but the composition of those communities was different when comparing old-growth forests (>120 years old) with both second-growth (30 to 70 years old), and conifer plantations (30 to 40 years old). In a review of 34 studies on the impacts of converting tropical forests to agricultural fields or vacant logged sites, Dunn (2004) concluded that logging did not decrease ant species richness overall, as did converting to agriculture.

The use of insecticides in management activities

The effects of chemical methods of insect control on ant populations have also been investigated. Few studies have demonstrated that insecticides have long-term effects on ant populations or ant communities in grassland or forest systems. Several studies of aerial applications of Dimlin 2F®, Dimlin 25W®, and Sevin 4-oil®, all used to control grasshoppers in grasslands, showed no long-term effect on diversity or abundance of ant populations (Catangui et al. 1996). They did show that in one study, however, the diversity of ants decreased in the first 13 to 19 days after treatment with the insecticide Dimlin 25W, but it recovered quickly to pretreatment levels. The five most abundant species of ants found in this study included *Lasius neoniger, Monomorium minimum, Solenopsis molesta, Tapinoma sessile,* and *Formica neogagates.* Wang et al. (2000) detected no change in the richness, diversity, abundance, or composition of ant species when considering the effects of the microbial insecticide *Bacillus thuringiensis* variety Kurstaki, which is used in gypsy moth management in eastern U.S. deciduous forests. This is not surprising since *Bacillus thuringiensis* is not reported to be toxic to ants (Rechcigl and Rechcigl 1999). Murphy and Croft (1990) studied the effect on forest ant species of carbaryl application for control of the western spruce budworm. They found that foraging by ants decreased in all plots, probably due to suboptimal foraging conditions; however, they noted a more rapid decrease occurred in the plots treated with insecticide. Ant foraging remained low for at least 76 weeks before rebounding. Additionally they found that the diversity of ant species decreased in sprayed plots relative to non-treated control plots. Wiktelius et al. (1999) examined the effects of the organochlorine insecticides, lindane and endosulfan, on non-

target arthropods. Lindane reduced the numbers of collembola by 80% for an average of six weeks, spiders by 53% for 2.8 weeks, and ants by 64% for an average of 2.5 weeks. In this study endosulfan had no effect on overall arthropod abundance.

Impacts on the dominance hierarchy in ant communities

Dominance hierarchies in ant communities have been well documented (Hölldobler and Wilson 1990; Morrison 1996). Dominant ant species influence the composition and abundance of other ant species in the ecosystem through competition and interference behaviors. Morrison (1996) suggested that negative interspecific interactions helped maintain territories of dominant ant species though dominant species were sometimes positively associated with specific subordinate ant species. Several studies have found a relationship between the daily activities of ants and their position in the dominance hierarchy. Cerda et al. (1997, 1998) determined subordinate species were more active during the day when temperatures were extreme, whereas dominant species were more active during periods characterized by more moderate temperatures, the less stressful times of late afternoon and night. The thermal intolerance of the previously dominant species allowed the subordinate species to become more dominant than would be expected from their relative abundance and fighting abilities. Bestelmeyer (2000) also observed a trade-off between dominance and thermal tolerance in ant communities. Retana and Cerda (2000) examined the factors affecting community structure in the Spanish Mediterranean. The relative abundance of dominance groups showed a seasonal pattern relating to vegetation cover and temperature. In grasslands, subordinates increased and dominants decreased their relative abundance from spring to summer, but in shrublands and forests, the opposite pattern occurred. Kemel et al. (2001) examined the effect of low- and high-impact logging in Brazil on the dominance hierarchy of ants. At the genus and species level, both logging techniques affected the composition of the ant community by reducing the dominance of ants in the genus *Pheidole*. Vanderwoude et al. (1997) looked at the effects of fire regimes on ant community structure in Australia. The relative abundance of opportunistic species was positively related to fire frequency while typically dominant ants constituted more of the ant community in unburned sites. Samways et al. (1997) examined ant communities in relation to their distance from a major urban highway in Africa. Invasive *Solenopsis invicta* and *Pheidole* spp., which tend to become dominant in newly colonized areas, increased in abundance on clear-cuts as early as two months after cutting, whereas densities of native ant species were significantly reduced.

(Zettler et al. 2004). In this study, dominant species pre-adapted for disturbance appeared to influence the presence and abundance of the rarer species through competition.

Habitat fragmentation also affects ant communities. Braschler and Baur (2003) found that three years after initiation of a controlled experiment where they manipulated the degree of fragmentation, there was no difference between fragments and control plots in the density of ant nests. Six years after initiation of the experiment, however, the density of ant nests and the abundance of foragers were higher in large fragments than in large control plots. Ant nests occurred more frequently along the edge of fragments than in the core area. Persistence time of nests of the most abundant species, *Lasius paralienus,* was shorter in fragments than in control plots. Furthermore, persistence time was longer in nests situated close to the fragment edge than in nests in the core area.

Ants as Bioindicators

The question of whether ants can serve the role of a bioindicator or of an indicator of environmental change is important to future studies of biodiversity and the environmental impacts of disturbance. Indicator species have been defined as those that can be easily sampled, represent fairly diverse groups, have known relationships to the diversity of other taxa, and respond to environmental change similarly to other taxa (Agosti 2000; Oliver and Beattie 1996). One of the most noted use of ants as bioindicators is their use in mine reclamation sites (Andersen 1996; Majer 1983, 1996, 1992; Majer et al. 1984). Ants were tested as possible indicators because of their importance to soil fertility and structure. Ant abundance correlated positively with richness and diversity of plant species, percentage of cover, time since rehabilitation, percentage of litter cover, and the presence of large logs. Compared to the composition of the ant community in nearby native forests, generalist species were more common in the rehabilitation sites. Results indicated ant diversity and abundance were indicators of recovery and successful rehabilitation of bauxite mines. Peck et al. (1998) investigated whether ants are good bioindicators in agroecosystems by examining ant populations in agricultural fields. The abundance of ants was higher in field margins than in cultivated fields for all species found except for the invasive *Solenopsis invicta.* Ant abundance was correlated with tillage type, soil variables, and crop conditions. Ants appeared to be potential indicators of environmental change in agroecosystems, though their association with specific levels of disturbance in agroecosystems is unknown. However, New (2000)

observed no difference between the number of ant morphospecies in native grassland and disturbed sites in Australia. He theorized this was because either small-scale heterogeneity remained high enough for ant populations to coexist in a stable manner or ants were not be sufficiently sensitive to floristic change.

The potential use of ants as indicators of herbicide-induced environmental change in forests is due to several characteristics. As already discussed, ants are sensitive to soil, temperature, and moisture changes. Agosti et al. (2000) reported that many ants have narrow tolerances for changes in environmental factors and their populations may respond quickly. Ants have been used to reflect changes in environmental gradients such as net aboveground productivity (NAP). Kaspari et al. (2000) described ant density as an increasing function of NAP. Net aboveground productivity was converted to a measure of density and biomass of ant colonies that increased with summer temperatures and decreased with precipitation. Andersen (1997) noted that the predictive power of ants as bioindicators in land management is not possible at the species level, but may be possible at the functional level, which varies predictably with climate, soil, vegetation, and disturbance.

CONCLUSIONS

We have shown that there are few generalities that can form a foundation for a conceptual model of the effects of glyphosate herbicides in forest ecosystem structure and function. In the short-term, abundance or biomass of non-crop deciduous trees and herbaceous vegetation, species diversity, and species richness may be reduced by applications of glyphosate herbicides, but recovery begins within the first two to four years following treatment. There are exceptions to this rule, however, as some studies found no observed effect on the plant community or even an increase in plant cover or biomass resulting from herbicide treatments. In the long-term, species of non-crop woody and herbaceous plants are usually not eliminated, resulting in similar measures of plant species diversity and species richness between treated and non-treated forest stands. What does appear to differentiate sites treated with glyphosate herbicides from non-treated sites are differences in the height of non-crop deciduous plants, the percentage of cover and the stand density of herbaceous, deciduous, and coniferous plants, which usually are greater in non-treated sites. There should also be a net gain in conifer height, percentage of cover, and biomass in glyphosate-treated stands, which would be slowed in the presence of hardwood competitors. Conifers (red spruce/balsam fir) grow quickly once released.

Glyphosate herbicides used in forest management have not been found to be highly toxic to forest-inhabiting wildlife. The effects of glyphosate herbicides on amphibians and fish, for the most part, appear to be negligible. Indirect effects of glyphosate herbicides, by means of reduced herbaceous plant, shrub, and deciduous tree cover, on insects, birds, small mammals, and large mammals can result in short-term reductions in abundance, but usually not in declines in species richness or species diversity. Long-term effects are less common and possibly more subtle and difficult to detect than short-term effects. The one general rule appears to be that effects of glyphosate herbicides on forest ecosystem structure and function are variable and specific to the herbicide and the rate at which it is applied, to the geographic location, soils, and climate characterizing the specific forest landscape, and to the flora and fauna that make up the resident communities inhabiting the forest landscape. However, instead of calling for more site-specific studies that might add to the list of contradictory results, we suggest increased focus on studying the effects of glyphosate herbicides on ecosystem function responses such as net productivity and nutrient recycling. These potential impacts have not been well studied. In addition, one must be aware that long-term studies, which are difficult and costly to conduct, are paramount for elucidating effects of herbicides such as glyphosate on mammal morbidity and mortality. However, these studies should also focus on sub-lethal chronic effects, especially now that it has been suggested that a link exists between glyphosate exposure and incidence in human beings of non-Hodgkin's lymphoma, a form of cancer (Hardell and Eriksson 1999). However, there is strong debate about whether glyphosate does pose a risk to human beings and mammalian wildlife and currently there is no definitive evidence available to indicate that glyphosate is a carcinogen (USEPA 2000; Tatum 2004).

We hope this review of the current literature on the impacts of glyphosate herbicides and the importance of ant communities within the forest ecosystem has demonstrated the need to consider invertebrate communities when evaluating or implementing forestry management practices. The forest-harvest method can have long-lasting effects on the structure of the dominance hierarchy of ant communities, which could affect the ability of invasive species to become established within a forest landscape. The role of ants as predators and the potential negative or positive effects of forestry practices may have bearing on populations of pest insects and conservation biological control, soil modification, and plant biomass, plant species richness, and plant species diversity.

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