# Variation in Enantiospecific Attraction of *Ips avulsus* (Coleoptera: Curculionidae) to the Pheromone Ipsdienol in Georgia

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**ABSTRACT** In 2006, we tested the responses of the small southern pine engraver, *Ips avulsus* (Eichhoff) (Coleoptera: Curculionidae), to multiple-funnel traps baited with (+)-, (–)-, and (±)-ipsdienol. Three experiments were conducted in Georgia with all traps co-baited with one of the following lure combinations, respectively: experiment 1, ipsenol; experiment 2, lanierone and (–)-$\alpha$-pinene; and experiment 3, ipsenol, lanierone, and (–)-$\alpha$-pinene. Ipsdienol and lanierone are aggregation pheromones used by *I. avulsus*, whereas ipsenol is an aggregation pheromone used by the eastern fivespined ips, *Ips grandicollis* (Eichhoff), a sympatric species also breeding in pines. In all experiments, the highest catches of *I. avulsus* were obtained in traps baited with (±)-ipsdienol. The relative attractiveness of (+)-ipsdienol varied across the three experiments. When traps were co-baited with ipsenol, lanierone, and (–)-$\alpha$-pinene, catches of *I. avulsus* in traps baited with (+)-ipsdienol were high and no different from those in traps baited with (±)-ipsdienol. When traps were co-baited with lanierone and (–)-$\alpha$-pinene, catches in traps baited with (+)-ipsdienol were lower than those in traps baited with (±)-ipsdienol by ≈40%, whereas catches were reduced by ≈95% when traps were co-baited with ipsenol alone. We hypothesize that the observed variation in enantiospecific responses of *I. avulsus* to ipsdienol may be explained by variation in semiochemical context (i.e., different co-baits among the experiments) or seasonal variation.

**KEY WORDS** ipsdienol, enantiomers, *Ips avulsus*, semiochemical context, seasonal variation

Management programs for bark beetles rely heavily on monitoring tools such as semiochemical-baited traps because detection of bark beetles in wood products (e.g., dunnage) is difficult due to the cryptic nature of adults and immatures (Allen and Humble 2002). In the United States, multiple-funnel traps baited with tree volatiles and bark beetle pheromones are used in the Cooperative Agricultural Pest Survey and the Early Detection and Rapid Response program to detect a broad array of exotic insects associated with trees and wood products (USDA–APHIS 2007, Rabaglia et al. 2008). Operational mass-trapping programs targeting ambrosia beetles (Coleoptera: Curculionidae) at timber-processing sites in British Columbia, Canada, use multiple-funnel traps baited with ambrosia beetle pheromones and conifer volatiles (Lindgren and Fraser 1994). For several decades, a southwide pheromone-baited trapping program has provided information on population levels and trends for the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae), guiding management activities (Clarke 2001).

A critical feature of any operational monitoring program is an effective and affordable commercial lure (Strom et al. 2003). Currently, there is uncertainty concerning the cost-effectiveness of lures for many common species of bark beetles such as the small southern pine engraver, *Ips avulsus* (Eichhoff). *I. avulsus* is one of three species of *Ips* engravers common to southeastern United States that can cause significant economic losses to forest resources by killing southern pines (Connor and Wilkinson 1983). Spot infestations of trees killed by *Ips* engravers can occur in association with logging debris, drought, lightning strikes, and compacted soils, but they are generally short-lived. Ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) and lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) are pheromones produced by *I. avulsus* (Vité et al. 1972, Birgersson et al. 1995). Ipsdienol is attractive to both sexes of *I. avulsus* (Renwick and Vité 1972, Miller et al. 2005), with lanierone synergizing attraction to ipsdienol-baited traps (Birgersson et al. 1995, Miller et al. 2003, 2005).

The enantiomeric composition of ipsdienol used by *I. avulsus* is uncertain and may be an important consideration due to the high cost of ipsdienol lures with high optical purity (Strom et al. 2003). In Texas, Vité et al. (1978) found that catches of *I. avulsus* in traps

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baited with (*R*)-(–)-ipsdienol were greater than those baited with (*S*)-(+)-ipsdienol or (±)-ipsdienol (=racemic ipsdienol, 50:50 mix of the two enantiomers). All traps were co-baited with the kairomone, ipsenol (2-methyl-6-methylene-7-octen-4-ol), a pheromone used by the eastern fivespined ips, *Ips grandicollis* (Eichhoff) (Vité et al. 1972, 1976). Ipsenol synergizes attraction of *I. avulsus* to traps baited with (±)-ipsdienol (Hedden et al. 1976, Kohnle et al. 1994, Miller et al. 2005). Strom et al. (2003) found that catches of *I. avulsus* were greater in traps baited with (±)-ipsdienol than in those baited with (–)-ipsdienol when traps were co-baited with lanierone; (+)-ipsdienol was not tested. Kohnle et al. (1994) and Seybold et al. (1995) found that the enantiomeric (+):(–) ratio of ipsdienol produced by male *I. avulsus* in Texas and Alabama, respectively, was 90:10 and 75:25, respectively.

Our goal was to clarify the role of enantiomeric composition of ipsdienol on the attraction of *I. avulsus*, particularly when co-baited with lanierone and ipsenol. At present, the tertiary combination of (±)-ipsenol, (±)-ipsdienol, and lanierone is the most attractive lure blend for *I. avulsus* in southeastern United States (Miller et al. 2005). In three experiments, we determined the enantiospecific response of *I. avulsus* to ipsdienol with traps co-baited with 1) lanierone and (–)-α-pinene; 2) ipsenol; and 3) all three compounds. In addition, we monitored the responses of *I. grandicollis* to these blends when co-baited with ipsenol.

## Materials and Methods

Phero Tech International (Delta, BC, Canada; now Contech Enterprises Inc., Victoria, BC, Canada), supplied bubble-cap lures of (±)-ipsenol, (±)-ipsdienol, (+)-ipsdienol, (–)-ipsdienol, and lanierone (chemical purities, >98%). The enantiomeric ratios of ipsdienol in the (+)- and (–)-ipsdienol lures were 97:3 and 3:97 (+):(–), respectively. The release rates of ipsenol, ipsdienol and lanierone were ≈0.2, 0.2, and 0.02 mg/d at 22–24°C (determined by Phero Tech International). In addition, Phero Tech International supplied sealed ultrahigh-release plastic pouches containing α-pinene (200 ml) (chemical purity, >95%; enantiomeric purity, >95% (–), releasing α-pinene at a rate of 2–6 g/d at 25–28°C (determined by weight loss).

In 2006, three trapping experiments were conducted on the Oconee National Forest near Eatonton, GA (33.342° N, −83.488° W; elevation, 164 m above sea level) to determine the responses of *I. avulsus* to traps baited with (+)-, (–)-, and (±)-ipsdienol and various co-baits. The site consisted primarily of mature loblolly pine, *Pinus taeda* L., with some recent disturbance in the stand from prescribed burning. We used a behavioral choice type of experiment in a randomized complete block design for each experiment. Ten blocks of three 8-unit multiple-funnel traps (Phero Tech International) were set in a curvilinear array. Traps within blocks and between consecutive blocks were set 10–15 m apart. Each trap was suspended by rope between trees such that the collection cup of each trap was 0.2–0.5 m above ground level. No trap was within 2 m of any tree. Collection cups contained 150–200 ml of pink propylene glycol solution (Peak RV and Marine Antifreeze, Old World Industries Inc., Northbrook, IL) as a killing and preservation agent (Miller and Duerr 2008).

In each experiment, the following three treatments were randomly assigned to traps within each block of traps: 1) (+)-ipsdienol, 2) (±)-ipsdienol, and 3) (–)-ipsdienol. We used various combinations of lanierone, ipsenol, and (–)-α-pinene as co-baits in experiments 1–3. All traps in experiment 1 were co-baited with ipsenol whereas all traps in experiment 2 were co-baited with lanierone and (–)-α-pinene. In experiment 3, all traps were co-baited with the three compounds: ipsenol, lanierone, and (–)-α-pinene. (–)-α-Pinene was included in experiments 2 and 3 due to low trap catches of *I. avulsus* in experiment 1. Experiments 1–3 were conducted consecutively: 30 August–20 September, 20 September–31 October, and 31 October–28 November, respectively.

Data were analyzed using the SYSTAT, version 11.00.01 and the SigmaStat, version 3.1) statistical packages (Systat Software Inc., Point Richmond, CA). Trap catch data were transformed by ln(Y+1) to reduce heteroscedasticity (Pepper et al. 1997). After verification of normality and homoscedasticity, transformed data were subjected to analysis of variance (ANOVA) by using the following replicate and treatment as model components. The Holm–Sidak multiple-comparison procedure (Glantz 2005) was used to compare treatment means within each experiment. Voucher specimens of *I. avulsus* and *I. grandicollis* were deposited in the Entomology Collection, Museum of Natural History, University of Georgia (Athens, GA).

## Results

In experiment 1, the total catches of *I. avulsus* and *I. grandicollis* were 531 and 1,043, respectively. There were significant treatment effects of enantiomeric composition of ipsdienol on both species with traps co-baited with ipsenol (*I. avulsus:* $F_{2,18} = 93.23$, $P < 0.001$; *I. grandicollis:* $F_{2,18} = 6.36$, $P = 0.008$). The mean catch of *I. avulsus* in experiment 1 was greatest in traps baited with ipsenol and (±)-ipsdienol (Fig. 1A). Catches in traps baited with ipsenol and (–)-ipsdienol were greater than those in traps baited with ipsenol and (+)-ipsdienol but less than those in traps baited with ipsenol and (±)-ipsdienol (Fig. 1A). The mean catch of *I. grandicollis* was greater in traps baited with ipsenol and (±)-ipsdienol than in traps baited with either ipsenol and (–)-ipsdienol or ipsenol and (+)-ipsdienol, with no difference in mean catches between the two later treatments (Fig. 1B).

The total catch of *I. avulsus* in experiment 2 was 9,946, with a significant effect of enantiomeric composition of ipsdienol on catches of beetles in traps co-baited with lanierone and (–)-α-pinene ($F_{2,18} = 32.24$; $P < 0.001$). The mean catch of *I. avulsus* was

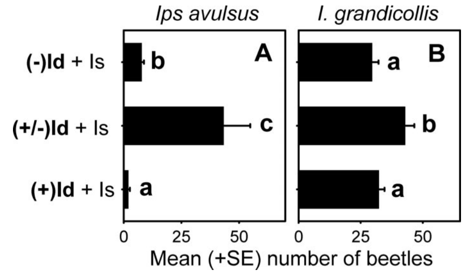

**Fig. 1.** Effects of (–)-, (+)-, and (±)-ipsdienol on attraction of *I. avulsus* (A) and *I. grandicollis* (B) to traps co-baited with ipsenol (experiment 1). Means followed by a different letter are significantly different at $P = 0.05$ (Holm–Sidak multiple comparison test). Id, ipsdienol; Is, ipsenol.

greatest in traps baited with lanierone, (–)-α-pinene and (±)-ipsdienol, whereas the addition of (–)-ipsdienol to traps co-baited with lanierone and (–)-α-pinene yielded the lowest mean catches (Fig. 2). Catches of *I. avulsus* in traps baited with lanierone, (–)-α-pinene and (+)-ipsdienol were intermediate between the other two treatments (Fig. 2). Only four *I. grandicollis* were captured in experiment 2.

In experiment 3, the total catches of *I. avulsus* and *I. grandicollis* were 22,476 and 64 beetles, respectively. There were significant treatment effects of enantiomeric composition of ipsdienol on both species with traps co-baited with ipsenol, lanierone and (–)-α-pinene (*I. avulsus:* $F_{2,18} = 262.78$, $P < 0.001$; *I. grandicollis:* $F_{2,18} = 4.216$, $P = 0.032$, respectively). The highest catches of *I. avulsus* were obtained in traps baited with the quaternary blends including either (±)-ipsdienol or (+)-ipsdienol, with no significant difference in mean catches between the two treatments (Fig. 3A). The lowest catches were in traps baited with the quaternary blend including (–)-ipsdienol. Catches of *I. grandicollis* were greater in traps baited with the quaternary blend including (±)-ipsdienol than in traps baited with the quaternary blend including (+)-ipsdienol (Fig. 3B). No other significant differences were observed.

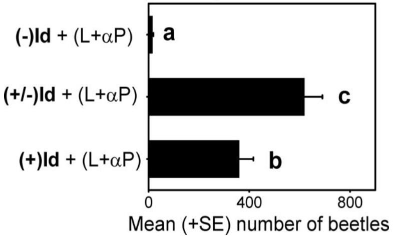

**Fig. 2.** Effects of (–)-, (+)-, and (±)-ipsdienol on attraction of *I. avulsus* to traps co-baited with lanierone and α-pinene (experiment 2). Means followed by a different letter are significantly different at $P = 0.05$ (Holm–Sidak multiple comparison test). Id, ipsdienol; Is, ipsenol; L, lanierone; αP, α-pinene.

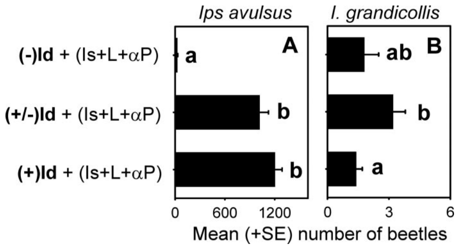

**Fig. 3.** Effects of (–)-, (+)-, and (±)-ipsdienol on attraction of *I. avulsus* (A) and *I. grandicollis* (B) to traps co-baited with ipsenol, lanierone, and α-pinene (experiment 3). Means followed by a different letter are significantly different at $P = 0.05$ (Holm–Sidak multiple comparison test). Id, ipsdienol; Is, ipsenol; L, lanierone; αP, α-pinene.

## Discussion

The role of enantiomeric composition of ipsdienol in the chemical ecology of *I. avulsus* is unclear. Initial studies identified the presence of ipsdienol in the hindguts of *I. avulsus* but not the enantiomeric composition of ipsdienol produced by beetles (Vité et al. 1972). Subsequent studies disclosed that male *I. avulsus* produce both enantiomers, favoring (+)-ipsdienol. Beetles reared on longleaf pine, *Pinus palustris* Mill., in Texas produced ipsdienol with an enantiomeric (+):(–) composition of 90:10 (Kohnle et al. 1994), whereas beetles reared on *P. taeda* in Alabama produced ipsdienol with an enantiomeric (+):(–) composition of 75:25 (Seybold et al. 1995). Vité et al. (1978) reported that (–)-ipsdienol was more attractive to *I. avulsus* than either (+)-ipsdienol or (±)-ipsdienol and suggested that (+)-ipsdienol interrupted responses of *I. avulsus* to (–)-ipsdienol. Similarly, Smith et al. (1990) reported that more *I. avulsus* were attracted to traps baited with (–)-ipsdienol than to traps baited with (±)- or (+)-ipsdienol at a composition ratio of 45:1:1 with *trans*-verbenol and *cis*-verbenol, respectively. At a composition ratio of 2:2.5:1 for ipsdienol, *trans*-verbenol and *cis*-verbenol, respectively, they found no difference in catches of *I. avulsus* in traps baited with (–)- or (±)-ipsdienol. In contrast, Strom et al. (2003) found that multiple-funnel traps baited with lanierone and (±)-ipsdienol caught more *I. avulsus* than traps baited with lanierone and (–)-ipsdienol in Louisiana, Florida, and Texas. (+)-Ipsdienol was not tested in their study. Direct comparison of the results of some of these studies is complicated by differences in the semiochemical co-baits attached to traps (among other factors). Traps were co-baited with ipsenol in Hedden et al. (1976) and Vité et al. (1978), lanierone in Strom et al. (2003), and *trans*-verbenol and *cis*-verbenol in Smith et al. (1990).

Our study attempted to determine the effects of both enantiomers of ipsdienol and (±)-ipsdienol on the attraction of *I. avulsus* to traps co-baited with ipsenol, lanierone, or both. Irrespective of co-baits, we found that (±)-ipsdienol performed as well as, if not better than, (+)-ipsdienol in attracting *I. avulsus* to baited multiple-funnel traps (Figs. 1–3). (–)-Ipsdienol did not perform anywhere near the level of (±)-ipsdienol. Our results are consistent with those of Kohnle et al. (1994), Birgersson et al. (1995), Strom et al. (2003), and Miller et al. (2005). There may be no need to use costly ipsdienol lures with high optical purity in a monitoring or detection program for *I. avulsus.*

We found significant variation in the relative attractiveness of (+)-ipsdienol to *I. avulsus* among the three experiments. In experiment 3, catches of *I. avulsus* in traps baited with (+)-ipsdienol were high and not different from those in traps baited with (±)-ipsdienol (Fig. 3). In experiments 1 and 2, catches of *I. avulsus* in traps baited with (+)-ipsdienol were lower than those in traps baited with (±)-ipsdienol by 95 and 42%, respectively (Figs. 1 and 2). In all three experiments, catches of *I. avulsus* in traps baited with the antipode, (–)-ipsdienol were consistently low although catches of beetles in traps baited with (–)-ipsdienol were higher than those in traps baited with (+)-ipsdienol in experiment 1. The opposite was true in experiments 2 and 3 where catches were higher in traps baited with (+)-ipsdienol than in traps baited with (–)-ipsdienol.

At this time, we are unable to adequately explain the variation in relative attractiveness of (+)-ipsdienol to *I. avulsus* among the three experiments. Intrapopulation variation in pheromone production and responses is common among bark beetles (Borden et al. 1986) and higher than that found in lepidopteran species (Schlyter and Birgersson 1989). Within a population, the responses of bark beetles can be affected by various factors such as the presence of semiochemicals produced by other species (Byers 1989). Such contextual information should provide responding beetles with some predictable measure of reproductive success relative to other choices. Exploiting information on the location and suitability of ephemeral hosts such as stressed trees or recent blowdown, even when conveyed by heterospecifics, could offset negative effects from the likelihood of interspecific interactions.

The different scenarios represented by the different baits may require different levels of enantiospecificity by *I. avulsus* at the tree scale. It is possible that the variation in responses by *I. avulsus* to (+)-ipsdienol relates to fitness parameters conveyed by contextual information in the form of co-baits. The strong preference by *I. avulsus* for (±)-ipsdienol over (+)-ipsdienol in experiment 1 may indicate an avoidance of sites potentially occupied by a competing species, one using (+)-ipsdienol as a pheromone. The lack of the pheromone, lanierone used by *I. avulsus* could indicate that the site is dominated by a competing species therefore requiring strong enantiomeric acuity to minimize interspecific conflicts yet still occupy a niche adjacent to those used by other species. The presence of lanierone in experiment 2 may indicate a greater presence of *I. avulsus* at the production site, thereby reducing the strong need for enantiospecificity at the spatial level of 10–15 m as used in our study. The presence of both ipsenol and lanierone may eliminate the need for any interruption from (+)-ipsdienol. A competing species may not be associated with that assemblage of pheromones at the spatial level of landing at a site on a tree. Such cues may indicate the broad availability of host resources for mating, egg laying and larval development.

At present, we do not know of any species other than *I. avulsus* that might use primarily (+)-ipsdienol in southeastern United States. In southeastern United States, *I. avulsus* is often associated with sixspined ips, *Ips calligraphus* (Germar) as well as *D. frontalis* and *I. grandicollis* (Švihra et al. 1980, Wagner et al. 1985). Paine et al. (1981) found that *I. calligraphus* colonized the middle bole of standing *P. taeda,* overlapping broadly with *I. avulsus.* When found together on the same tree, *I. avulsus* occupied less surface area than when it was not in association with *I. calligraphus.* In contrast, the area occupied by *I. calligraphus* was unaffected by the presence of *I. avulsus. I. grandicollis* can be found in low numbers on various portions of the trunk but seems to be more common in large branches of the lower crown (Švihra et al. 1980, Paine et al. 1981).

As with *I. avulsus,* little is known about the role of enantiomeric composition of ipsdienol in the chemical ecology of *I. calligraphus.* Like *I. avulsus,* initial studies identified ipsdienol in the hindguts of male *I. calligraphus* but not the enantiomeric composition of ipsdienol (Renwick and Vité 1972). Subsequent studies disclosed that male *I. calligraphus* reared on *P. palustris* in Texas produced ipsdienol with an enantiomeric composition of 23% (+) (Kohnle et al. 1994). In the same study wherein Vité et al. (1978) reported that (–)-ipsdienol was more attractive to *I. avulsus* than either (+)-ipsdienol or (±)-ipsdienol, (–)-ipsdienol was reported to be more attractive to *I. calligraphus* than either (+)-ipsdienol or (±)-ipsdienol. Discrepancies with enantiomeric preferences of *I. avulsus* also may exist with *I. calligraphus.* Kohnle et al. (1994) found that both *I. avulsus* and *I. calligraphus* are attracted to (±)-ipsdienol in a dose-dependent manner.

There is evidence of limited cross-attraction between *I. calligraphus* and *I. avulsus* to host material colonized by either species (Birch et al. 1980, Švihra et al. 1980). Cross-attraction between the two species is not surprising due to the ephemeral and unpredictable nature of host material (Alcock 1982) and the adjacency of niche preferences on the same trees (Paine et al. 1981). At some point individuals of both species must discriminate among con- and heterospecific galleries to minimize interspecific conflicts and maintain reproductive isolation. Such decisions probably involve multiple cues and signals from chemical, acoustic, or visual modalities (Birch et al. 1980, Seybold et al. 1995). Additional compounds in the pheromone blend of both species could allow for short-range species separation, irrespective of ipsdienol enantiomeric composition. In addition to potential differences in enantiomeric ratios of shared components, the southern *Ips* species have qualitative blend differences in pheromone blends. *I. calligraphus* uses ipsdienol and *cis*-verbenol, *I. avulsus* uses ipsdienol and lanierone, and *I. grandicollis* uses ipsenol alone

(Renwick and Vité 1972; Vité et al. 1972, 1976; Birgersson et al. 1995, Miller et al. 2003, 2005).

Alternatively, the variation in relative attraction of *I. avulsus* to traps baited with (+)-ipsdienol that we observed across our three experiments may relate to temporal or seasonal factors. Several studies have observed seasonal variability in bark beetle responses to pheromones (Birch 1974, Roberts et al. 1982, Teale and Lanier 1991), related to reproductive stage, physiology, age, symbionts (Atkins 1966, Bennett and Borden 1971, Hunt and Borden 1990, Gast et al. 1993), population density (Wallin and Raffa 2002), abiotic conditions (Borden 1967) and host condition or resistance (Renwick et al. 1976, Stephen and Paine 1985, Seybold et al. 1995, Wallin and Raffa 2002).

In our study, experiments 1–3 occurred consecutively in 2006: 30 August–20 September, 20 September–31 October, and 31 October–28 November, respectively. During the first time period, enantiospecificity against (+)-ipsdienol was strong with little, if any attraction to traps baited with (+)-ipsdienol. During the second period, attraction to (+)-ipsdienol was half of that to traps baited with (±)-ipsdienol, whereas by the third period (+)-ipsdienol was just as attractive as (±)-ipsdienol. It is possible that beetles were less discriminatory as the season came to a close, probably due to limited probability of finding high quality hosts before winter sets in. Late in the season, beetles may respond to any cue or signal with a significant component of (+)-ipsdienol while still avoiding sites producing primarily (–)-ipsdienol. Seasonal variation may explain variation in enantiomeric responses of *I. avulsus* observed in other studies as well (Vité et al. 1978, Strom et al. 2003).

Seasonal-based variation in enantiospecific responses has been reported for the pine engraver, *Ips pini* (Say). Steed and Wagner (2008) found that *I. pini* in Arizona and Montana exhibited a stronger preference for (–)-ipsdienol in summer compared with spring. When co-baited with lanierone, catches of *I. pini* to traps baited with (±)-ipsdienol were not significantly different from those in traps baited with (–)-ipsdienol in the spring. By the summer, catches in traps baited with (–)-ipsdienol where significantly higher than those in traps baited with (±)-ipsdienol.

Future research should determine the contextual and seasonal patterns of enantiomeric responses in *I. avulsus* as well as other species, and the fitness consequences of such patterns. Variation in bark beetle responses to pheromonal cues and signals has potential consequences for pest management programs. Temporal patterns of variation would suggest that the most efficacious lure in a management program may not be independent of date of deployment. Contextual patterns of variation would suggest that deploying novel or untested combinations of pheromones may have unintended, negative consequences on trap catches. Understanding the evolutionary ecology of bark beetle communication systems should aid in predicting and managing impacts arising from global climate change and invasions of exotic species, as well as changes in land management practices.

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