

Declining abundance of American ginseng (Panax quinquefolius L.) documented by herbarium specimens

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ABSTRACT

American ginseng (Panax quinquefolius L.) is a native North American forest herb whose roots have been collected for their reputed medicinal properties and exported to international markets for nearly 300 years. Numerous anecdotal reports suggest declining abundance throughout its range, and the species is currently listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora. This study examines the putative decline of American ginseng over the last 150 years in 19 US states by using data from herbarium specimens. For successive time intervals, we calculate the numbers of American ginseng specimens in addition to the numbers of specimens of related taxa that are not commercially harvested. The proportions of American ginseng specimens from adjacent time intervals are then examined for significant changes. An additional analysis evaluates the potential for species overrepresentation in the database due to species collection bias. Despite evidence of preferential collection of American ginseng, the proportion of American ginseng specimens declined significantly through time for six northern states. This result is consistent with a long and intense history of harvest, extensive deforestation in northern regions of the United States, and slow regeneration of American ginseng.

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1. Introduction

The conservation of threatened species requires not only accurate assessment of their current status, but also consideration of long-term trends in distribution and abundance, and evaluation of possible causes of declines. This historical context can provide direction for management plans, yet past distribution and abundance patterns are often scarcely documented and difficult to reconstruct. Natural history museum specimens provide one of the few sources of information with sufficient historical timescale and geographic coverage to allow investigation of range-wide changes in species' abundance. However, few studies have drawn on this source of information, in part because of the problems inherent in specimen data. These include species collection bias (i.e., the preferential collection of particular species) as well as variable collecting effort in time and space (Burgman et al., 1995; MacDougall et al., 1998; McCarthy, 1998; Ponder et al., 2001; Delisle et al., 2003). These biases could affect the amount, identity and geographical representation of specimens in a museum and confound the detection of any natural changes in distribution and abundance. Here, we develop a method to reduce collection biases in specimen data by comparing a species of interest to a set of "reference" taxa (Flinn, 2000; Hedenäs et al., 2002). We apply this method to investigate long-term trends in relative abundance of American ginseng, a species of biological, cultural and economic interest.

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American ginseng is an herbaceous perennial plant native to deciduous forests from southern Quebec and Minnesota, south to Louisiana and Georgia (Gleason and Cronquist, 1991; Anderson et al., 1993). Life history traits such as low seedling recruitment, slow individual growth and long prereproductive periods make this species especially vulnerable to disturbance (Lewis and Zenger, 1982; Charron and Gagnon, 1991; Nantel et al., 1996). Commercial harvesting of American ginseng roots began in the early 18th century, when European colonists recognized its similarity to the Asian species highly valued in traditional medicine (Schorger, 1969). Trade quickly flourished, and by the mid-19th century annual exports to international markets frequently exceeded 170 metric tons. Exports peaked in the 1880's and then sharply declined in the following decades apparently due to diminishing numbers of wild populations (Carlson, 1986). This encouraged a transition to cultivated roots. Although cultivation has lessened the pressure on wild populations, the collection of wild roots continues because their distinctive morphology commands a much higher price on Asian markets (Robbins, 1998; Robbins, 2000; Hankins, 2000). At the close of the 20th century, the US exported an average of 60 metric tons annually, with over 95% going to Asian markets (Robbins, 2000). Currently, 19 of the 34 US states that report wild populations of American ginseng are approved to export roots (Gabel, 2006, Fig. 1), with the greatest quantities coming from Kentucky, West Virginia and Tennessee. Although early harvesters were predominantly hunters, trappers, settlers and native Americans, harvesting has now become a longstanding tradition and important means of supplemental income for many rural households (Robbins, 1998, and citations therein). Therefore, harvest intensity and export quantities in any given year can fluctuate with local and Asian economies (Robbins, 1998), as well biological and environmental factors affecting supply.

As harvesting continued into the 20th century, increasing concern over the species' rarity resulted in listing it as an Appendix II species in the 1973 Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). This listing requires signatory countries to determine that materials destined for export were collected legally and without detriment to wild populations. In the United States, CITES policy is the responsibility of the Secretary of the Interior who acts through the US Fish and Wildlife Service (specifically the Division of Scientific Authority and the Division of Management Authority). For all states requesting export, these divisions annually review the non-detriment finding. In states covered by our study, only Michigan and Massachusetts are restricted from export (Fig. 1).

Numerous anecdotal reports over the past 200 years suggest that this species is declining in abundance (Michaux, 1805; Stanton, 1892; Schorger, 1969; Kalm, 1987, The English version of 1770). Indirect evidence, such as demographic models and the decreasing stature of herbarium specimens throughout the past century, also suggest negative impacts of harvest (Nantel et al., 1996; McGraw, 2001; Van der Voort and McGraw, 2006). Still, the extent, location and timing of population declines, as well as the relative influences of harvesting, habitat loss, and other factors such as deer browsing



Fig. 1 - Status and predominant range of American ginseng in the United States (the species is not known to occur in Florida). States with diagonal cross hatching indicate significant decreases in the relative frequency of American ginseng herbarium specimen collections from the mid-19th century to the mid-20th century (superscript 1), from the early 20th century to the 21st-century (superscript 2), or both transitions (superscript 1 and 2). States with vertical bars (and Minnesota at transition 2) show significant increases in the relative frequency of ginseng collections during one of the above transitions (superscript 1 or 2) and states with stippling show no significant changes. States without shading were not included in the study due to limitations of herbarium specimen sample sizes. Underlined states are those federally approved to export wild-collected roots.

(Furedi and McGraw, 2004; McGraw and Furedi, 2005) remain difficult to disentangle.

This study uses herbarium specimen data to examine changes in the relative abundance of American ginseng in 19 US states over the past 150 years. For successive time intervals, we compare herbarium specimen collection rates of American ginseng to collection rates of four other species: Panax trifolius L., Aralia hispida Vent., A. nudicaulis L., and A. racemosa L. These species are morphologically similar and closely related to American ginseng within the family Araliaceae (Wen and Zimmer, 1996; Holmgren, 1998). They also share wooded habitats (Gleason and Cronquist, 1991), and sometimes co-occur with American ginseng (particularly A. nudicaulis; personal observation). An important difference, however, is that the reference species are not commercially harvested. Thus, any changes in the relative abundance of American ginseng due to harvest pressure should be evident in this study. We also analyze whether the specimen data show bias due to preferential collection of a particular species. These techniques allow us to address the following questions: (1) How has the relative abundance of American ginseng changed over the past 150 years? (2) When and where have declines occurred? and (3) How are the data influenced by collection biases?

2. Materials and methods

2.1. Herbarium specimen data

For each herbarium contacted, we requested herbarium specimens or label data for all holdings of American ginseng and the four reference species, Panax trifolius, Aralia hispida, A. nudicaulis, and A. racemosa. For each specimen, we recorded the species, the location and date of collection, and the collector's name. Prior to our data analysis, we removed all duplicates (defined as multiple specimens of the same species that were collected in the same location and on the same day by the same collector). The database included all specimens with sufficient label information supplied by the following 85 herbaria located throughout the natural range of American ginseng (herbarium acronyms follow) (Holmgren and Holmgren, 1998): ABFM, ALBC, ALMA, APCR, AUA, AUB, BEREA, BLH, BRIT, BUF, BUT, CHARL, CLEMS, CM, CMC, CUS, DOV, DHL, DUKE, EKY, ETSU, EVMU, F, FUGR, GA, GH, GMUF, GSW, HXC, IA, ILLS, IND, IRP, ISC, ISM, JHWU, JMUH, KY, LCDI, LSC, LYN, MCTC, MCTF, MGR, MICH, MIL, MIN, MISS, MO, MRD, MSC, MUR, NCSC, NCU, ND, NEBC, NM, NY, NYS, ODU, OS, PAM, SMS, Southeast Wisconsin Regional Planning Commission, SYRF, TENN, UAM, UARK, UMBS, UMO, UNA, USCH, UWGB, UWL, VDB, VMIL, VPI, WBIS (http://www.botany.wisc.edu/wisflora/overview/index.asp; Last access March 2006), WILLI, WIS, WMU, WNC, WSCH, WUD, and WVA.

2.2. Analysis of changes in relative abundance

To measure changes in relative abundance of American ginseng specimens over time, we examined the proportion of American ginseng specimens in the entire collection for each of three successive time intervals: pre-1900, 1900-1949 and 1950-2001. These broad intervals allowed statistical testing between one or both time transitions (i.e., between intervals 1 and 2 or between intervals 2 and 3). G-tests of independence evaluated the association between the proportion of American ginseng specimens and the time interval. In the 2×3 tables, an experimentwise error rate α (Sokal and Rohlf, 1995) was applied for comparison of proportions in adjacent time intervals. When a time interval lacked sufficient data for a 2×3 test, it was pooled with an adjacent interval in a 2×2 table (Sokal and Rohlf, 1995). Insufficient data for a statistical test was defined as any cell in which the expected number of observations fell below five (Sokal and Rohlf, 1995). We performed all analyses for each state separately to facilitate application to the harvest and conservation practices regulated by state governments. We also wished to finely resolve any regional trends, and a state-by-state analysis was the smallest level of resolution permitted by the dataset (i.e., not all specimens had identifiable locations below the state level).

2.3. Analysis of collection biases

Several additional analyses evaluated how effectively our methods controlled for collection biases. In order to assess how the choice of individual reference species may have influenced the patterns we observed, we examined the proportions of American ginseng using each reference species separately. We also examined the consistency of temporal trends in specimen abundance among the reference species by calculating pairwise product-moment correlations of the numbers of specimens per decade within each state. Significant positive correlations would suggest that fluctuations in collecting effort affected all species similarly.

To identify potential bias due to preferential collection of a particular species, we focused on the extreme cases where collectors were represented in the database by multiple collections of a single species (hereafter called the subset). Thus, our subset consisted of all five species, but each collector in the subset was represented by multiple specimens of one of the five species. These instances could occur by sampling error of herbarium specimens, or they could indicate collectors who preferentially collected one of the species. A significant difference in the proportions of species in the subset relative to the entire database could indicate preferential sampling of a species in the subset. This may in turn suggest the direction of bias in the full dataset. Thus we compared the proportion of American ginseng in the subset to its proportion in the entire database with 2×2 contingency tables for all dates pooled and for the three time intervals individually. We also removed American ginseng from the analysis and compared the proportions of the four reference species in the subset to their proportions in the main database with a 4 × 2 contingency table for all dates pooled.

3. Results

3.1. Herbarium specimen data

Requests for specimen loans or label data yielded approximately 12000 records ranging across eastern North America and from the mid-19th century through 2001. Nineteen states had sufficient numbers of herbarium records in the database to analyze changes in relative species abundance over time (Fig. 1). Specimens collected before 1900 often had the lowest representation in the database (Fig. 2). Consequently, low sample sizes required pooling the first and second time intervals for Arkansas, Georgia, Kentucky, North Carolina, Tennessee, Virginia, and West Virginia. The second and third intervals in Massachusetts were pooled because of low collections of ginseng in the third interval. States within American ginseng's range that lacked enough herbarium specimens within our database to permit any testing were Alabama, Connecticut, Delaware, Louisiana, Maryland, Maine, Mississippi, New Hampshire, New Jersey, Rhode Island, and South Carolina (Fig. 1).

3.2. Changes in relative abundance over time

For six states across a broad region of the Northern US, the proportion of American ginseng specimens declined significantly over time (Figs. 1 and 2). Declines occurred between pre-1900 and 1900–1949 for Michigan (G = 6.85), Minnesota (G = 14.5), and New York (G = 14.5); between 1900–1949 and 1950–2001 for Wisconsin (G = 9.6); and between both sets of intervals for Pennsylvania (G = 13.5 and 7.2) and Vermont (G = 5.9 and 6.3; p < 0.05 for G > 5.0, p < 0.01 for G > 7.9). In con-



Fig. 2 – Herbarium specimen collection curves for all states examined. Numbers of specimens per decade are plotted for American ginseng (*Panax quinquefolius*; solid diamonds and bold line), P. trifolius (stars), Aralia hispida (open squares), A. *nudicaulis* (solid triangles), and A. *racemosa* (open triangles). For each state, the proportion of American ginseng specimens in each 50 or 100 year time interval (separated by dashed lines) is indicated. The total number of specimens over all five taxa (*n*) is also indicated for each interval. Adjacent time intervals with significantly different American ginseng proportions are indicated by different superscript letters. The first eight states (Indiana through Vermont) show significant changes in the proportion of American ginseng collections across one or more adjacent time intervals; the remaining states show no significant changes across time intervals.

trast, the proportion of American ginseng specimens increased in Indiana between pre-1900 and 1900–1949 (G = 6.6); and in Iowa (G = 8.4) and Minnesota (G = 35.6) between 1900–1949 and 1950–2001.

3.3. Collection biases

The four reference species showed strong correspondence in numbers of specimens per decade within states (Fig. 2). Most of the pairwise correlations between species (88%; 67 of 76 across all 19 states) were significant and positive, with a mean correlation of 0.71. Thus, temporal trends in collecting effort appeared to affect the four reference species similarly. This result indicates that a substantial portion of collecting effort can be controlled by examining proportional changes of American ginseng across time intervals.

As a consequence of the strong species correlations, analyses using each reference species separately gave highly similar results to the tests with reference species pooled. Out of 94 tests performed, 80 (85%) matched the pooled analyses for the respective states and intervals tested (i.e., non-significant changes remained non-significant, and significant changes remained significant in the same direction). Eleven tests indicated non-significant changes across intervals that were significant in the pooled analyses, but 10 of these still maintained the same direction of change. The remaining three tests indicated significant increases across intervals that were not significant in the pooled analyses (Kentucky



Fig. 2 – continued

using A. nudicaulis; Virginia using A. hispida or A. racemosa), but the direction of change was consistent with the pooled analyses in all cases.

The representation of American ginseng specimens in the subset compared to the entire database revealed a significant collection bias toward the overrepresentation of American ginseng by single-species collectors. The proportion of American ginseng specimens was significantly higher in the subset (38%, 177 specimens) than in the entire database (17%, 1433 specimens; G = 113, df 1, p < 0.001), whereas the subset and the entire database had comparable proportions of the reference species (A. hispida, 17% vs. 15%; A. nudicaulis, 41% vs. 37%; A. racemosa, 26% vs. 29%; and P. trifolius, 17% vs. 18%; G = 3.1, df 3, p > 0.40). Further analyses revealed that American ginseng was not significantly overrepresented in the time period up to 1900 (G = 0.95, df 1, p > 0.1) but was significantly overrepresented during 1900-1949 (G = 3.9, df 1, p < 0.05) and particularly during 1950–2001 (G = 133.5, df 1, p < 0.001; Fig. 3).

The overrerepresentation of American ginseng in the subset was influenced by the presence of several collectors who collected high numbers of American ginseng specimens. For example, no collector was represented by more than five specimens of a reference species, whereas six American ginseng collectors were represented by six to 23 specimens each. This large difference emerged even though there were substantially fewer American ginseng collectors (n = 50) than reference species collectors (n = 128) in the subset. Therefore, it is likely that the collectors of 6-23 specimens of American ginseng represent collection bias rather than a chance sampling event. We explored the effects of this apparent bias by removing the American ginseng collectors with 6-23 specimens (66 total specimens from MN, MO and TN collected from 1984 onward). This removal had little effect on the overrepresentation of American ginseng in the subset during 1950–2001 (G = 34.5, df 1, p <0.001), and did not change the outcome of the relative abundance analyses for MO or TN. Minnesota, however, changed from a significant increase in the proportion of American ginseng specimens in the transition between 1900-1949 and 1950-2001 to no significant change between those intervals (G = 2.6, df 1, p > 0.1). Further investigation



verified that the Minnesota collectors were exclusively collecting uncommon species like American ginseng in order to document populations (personal communication, Minnesota Natural Heritage).

4. Discussion and conclusions

4.1. Declining abundance of American ginseng

Herbarium specimen data from the past 150 years revealed significant declines in the proportion of American ginseng specimens across six northern US states (Figs. 1 and 2). These declines were apparent despite the likely overrepresentation of American ginseng in the database due to collection bias during the last 100 years. In effect, this bias would generate a highly conservative analysis that underestimates decreases in the relative abundance of American ginseng. Although herbarium specimens only indirectly represent natural abundance, the simplest explanation for declines in the proportion of American ginseng specimens is a change in the relative abundance of American ginseng that has lowered the probability of encountering it in the wild. This relative decrease could reflect changes in rates of population growth, establishment or local extinction; and it could occur through a decrease in American ginseng populations, an increase in populations of the reference taxa, or both. In any scenario, it is likely that the declines reflect harvest pressure and/or other ecological factors that have affected American ginseng and the reference species differentially.

4.2. Location and timing of declines

Declines in the relative abundance of American ginseng appear localized to the northern states rather than the southern and midwestern parts of the species' range. However, low sample sizes before 1950 were common in several southern states and probably decreased the likelihood that proportions in the sample reflect natural proportions. This was particularly true for Arkansas, Georgia, Kentucky and Missouri, where one of the intervals had 20 or fewer specimens (Fig. 2). The remaining intervals across all states generally had considerably larger sample sizes (range = 23–991; mean n = 186).

Collection bias has also influenced these data substantially. In this study, a preponderance of collectors appeared to focus on collecting American ginseng, and this overrepresentation increased dramatically in the 20th century (Fig. 3). Although we only identified the extreme cases of single-species collectors, this bias affected the entire database; within each state there are examples of individuals who contributed substantially higher proportions of American ginseng in their collections than the majority of collectors in the same state.

Collection bias could also run in the other direction. Collectors might avoid collecting American ginseng because of increasing perceptions of rarity. Such a bias would have the potential to contribute to the regional declines we observed. To examine this possibility further, we tested the proportion of American ginseng in the database for the combined years of 1960-1979 against the proportion for the combined years of 1980-2001. We chose these intervals because of the development of many Natural Heritage Programs after 1980 (http://natureserve.org/visitLocal/usa.jsp). These programs collect and manage biodiversity information, particularly on rare flora and fauna. If this bias is present, it might be strongest when knowledge and interest in rare flora are heightened. Interestingly, we found a highly significant increase in the percentage of American ginseng collections in the last two decades (from 6% to 14%, G = 25.7, df 1, p < 0.001) for the collective group of six northern states exhibiting significant declines over at least one time transition. Although low sample sizes prevented tests for individual states, the 1980's (in Michigan, New York, Pennsylvania, and Vermont) or 1990's



Fig. 3 – The proportion of American ginseng specimens in the single-species collectors subset (see text for explanation) compared to the proportion of American ginseng specimens in the whole database for each of three time intervals.

(Minnesota) were the decades that contained the highest proportions of ginseng collected in their respective 50-year intervals (often twofold or greater increases). For Vermont and Pennsylvania, the increase during 1980-1989 was not great enough to impact the overall decline from 1900-1949 to 1950–2001. We did not find a significant increase in recent collections for the collective group of states lacking significant declines (from 33% to 34%, G = 0.08, df 1, p > 0.50). These results argue against the possibility that the perception of ginseng's rarity in the north has hindered recent herbarium specimen collections and caused the significant declines. Undoubtedly, there are collectors who avoid collecting American ginseng because of its perceived rarity, but their influence is not apparent in the data. Thus, indications from both the subset (Fig. 3) and recent collecting patterns suggest a predominant trend of increasing collection with increasing rarity.

This type of collection bias may have contributed to a lack of significant declines in Ohio and Massachusetts. Ohio also exhibits the "uncharacteristic" rise in the proportion of American ginseng collections in the 1980's (again almost doubling in proportion compared to any other decade in the last interval). Over half of these collections were made by botanists working for the state. Likewise, Massachusetts shows a spike in this decade, although the percentage of ginseng collections are extremely low throughout all decades in this state. This makes the assessment of trends problematic, but also suggests a very low natural abundance throughout the last 150 years. Ultimately, collection bias in these data produced a highly conservative analysis where significant increases may be partially or wholly artifactual, and decreases are likely to be underestimated.

A lack of detailed information about historical changes in harvest patterns and the natural abundance of these species leaves many possible explanations for the apparent difference between the northern and southern regions. Ecological theory would predict that American ginseng would have been more abundant at its range center in southern Appalachia, making populations in this region more resilient to harvest pressure and habitat destruction (Brown, 1984; Lawton, 1993). Another important factor that is likely to contribute to an understanding of these results is the difference in deforestation patterns between northeastern states and mountainous southern Appalachia.

Five of the six states showing declines have pronounced changes across the first two time intervals; this time spans the peak and aftermath of agricultural clearing and commercial logging in these areas. In the northeast, forest clearing for agriculture proceeded throughout the 19th century, and many landscapes of New England, New York and Pennsylvania had lost as much as 80% of their forests to farm fields by 1900 (Smith et al., 1993; Hall et al., 2002; Whitney and DeCant, 2003). While subsequent farm abandonment allowed forests to reclaim much of this land, the large areas of forest in Ohio, southern Michigan and Wisconsin that were converted to farmland during the 19th century have mostly remained in agriculture (Williams, 1989; Whitney, 1994).

Also during the last half of the 19th century, commercial logging interest shifted to the upper Great Lakes region, particularly Michigan, Minnesota, and Wisconsin (Williams, 1989). There, the land was largely unsettled and highly favorable for the removal and transportation of timber. These factors, in combination with technological advances in lumber production, concentration of big-business control and extensive post-logging fires, resulted in the destruction of vast forest acreage. By 1920, the Northeast and Midwest lost an estimated 96% of their old-growth timber (Whitney, 1994; Reynolds and Pierson, 1923).

Deforestation patterns in deciduous forests of southern Appalachia differ in several important ways from these northern areas. The more rugged, mountainous landscapes of West Virginia, Virginia, Kentucky, North Carolina, South Carolina, Tennessee and Georgia were apparently less conducive to agriculture and settlement (Maizel et al., 1999), as well as large-scale logging. Lumbering in southern Appalachia often occurred as a small business (Yarnell, 1998), avoiding the relatively swift and spatially expansive deforestation patterns typical of the north (Williams, 1989). Therefore, it is likely that southern Appalachia retained a greater proportion of remnant forests than the northern landscapes in this study.

The differences in 19th-century deforestation patterns between these two regions could have profound impacts on the ability of forest species to recover after disturbance. Herbaceous understory plants like American ginseng would be expected to recolonize recovering forests more slowly in landscapes with less remnant forest cover and greater distances between remaining patches (Flinn and Vellend, 2005). Biological features of American ginseng that would contribute to a slow recovery include its slow growing habit, low seedling recruitment rates, long pre-reproductive period, and limited gene flow among populations (Charron and Gagnon, 1991; Grubbs and Case, 2004). Heavy deforestation coupled with ongoing harvest of American ginseng in the forest fragments would have exacerbated its difficult recovery in northern regions, probably causing many of the remaining populations to reach extinction thresholds. Thus, the differences between the northern and southern regions could represent a complex interaction among deforestation history, harvest, and a relatively poor ability of American ginseng to recover under the intense northern conditions. Comparative demographic analyses of American ginseng and the reference species, especially in areas of sympatry and under different disturbance regimes, could help clarify the likelihood of this hypothesis.

4.3. Implications for conservation

It is important to emphasize that our study focuses on proportional changes in the historical abundance of American ginseng, and not on absolute abundance. This has several implications. First, states showing no significant proportional decline (i.e., 13 of the 19 states in this study) could theoretically have a lower abundance of ginseng than states with significant declines. Furthermore, in states without proportional declines, American ginseng could have declined in concert with the reference taxa, a pattern that would not be detected by this study. Lastly, factors contributing to the historical decline of American ginseng may or may not be important causes of current declines. For example, deer browse has recently become an important conservation concern for American ginseng and other native herbs (Furedi and McGraw, 2004; Knight, 2004; McGraw and Furedi, 2005). For these reasons, a lack of significance in this study does not imply the absence of a current conservation concern. Ongoing efforts to evaluate and monitor populations are essential for understanding the effects of harvest as well as other threats. These analyses should include populations in the central and peripheral portions of its range for the most effective management strategies.

Many northern states have also reported relatively low annual harvests of wild roots in recent years (Pat Ford, the Division of Scientific Authority, US Fish and Wildlife Service, personal communication). Although social and economic factors as well as natural abundance influence annual variation in harvests (Robbins, 2000; McGraw et al., 2003), these export records are consistent with the hypothesis that northern populations have been particularly compromised. Of the states showing significant declines, Michigan is the only state to ban export. Our data suggest that a re-evaluation of other northern regions may be necessary. Of particular concern are Pennsylvania and Vermont, which show steadily decreasing proportions of American ginseng across both sets of time intervals.

4.4. Applicability of methods using specimen data

Absolute numbers of collections varied considerably across decades (Fig. 2) and this variation likely represents fluctuations in field collection and herbarium acquisition effort rather than changing abundances of species. This result is consistent with other studies tracking the collection of herbarium specimens through time (e.g., Hedenäs et al., 2002; Delisle et al., 2003; Prather et al., 2004a), and it emphasizes the need to control for collecting effort in time and space. As in the present study, the strong correlations in temporal trends among species within states indicates that controlling for collection effort is possible and effective. Collection bias, however, is more difficult to control. In general, studies focusing on rare or high-profile species may frequently encounter species-collection bias and, as seen in this study, this bias may increase over time as the taxon gains greater interest. Our data are consistent with other discussions of a recent shift in the emphasis of specimen collection from floristic and general-purpose collection to special-purpose collection (Burgman et al., 1995; Prather et al., 2004a; Prather et al., 2004b).

Other studies have successfully used reference taxa to control for collection effort, but in ways that differ from the present study. For example, Delisle et al. (2003) used five native non-invasive species to track the spread of six invasive species with specimen data. Hedenäs et al. (2002) used randomly selected herbarium specimens within a geographic region to document temporal changes in a moss flora in Sweden. Ponder et al. (2001) examined the reliability of distributional data for narrow-range taxa by comparing their distributional statistics to wide-ranging "background taxa." The diverse character and goals of these studies demonstrate the broad applicability of techniques that employ reference taxa and museum specimens. These techniques have the potential to yield information that is otherwise unavailable and highly useful in conservation.

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