A GLOBAL TREND IN BELOWGROUND CARBON ALLOCATION: COMMENT

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Gower et al. (1996) have questioned the validity of using a global-scale relationship between litterfall and belowground carbon (C) allocation (Raich and Nadelhoffer 1989) at stand and regional scales. We encourage attempts to understand better the controls on C allocation to roots in forests, including efforts to evaluate the potentials and limitations of C budgets for this purpose. However, the tests of our C-balance model that were presented by Gower et al. use inappropriate comparisons and the conclusions they drew are unwarranted. In addition, they misinterpret and misapply our C-budgeting models and their conceptual bases. Therefore, we clarify our approach to estimating belowground C allocation (Raich and Nadelhoffer 1989, Nadelhoffer and Raich 1992) and highlight problems with the tests of our models as conducted by Gower et al.

The issue in question is whether simplified soil C budgets can be used to estimate total root carbon allocation (TRCA, the annual rate at which assimilated C is allocated to producing and maintaining roots and mycorrhizae) in forest ecosystems. The conceptual model underlying the statistical model we used to predict TRCA at global scales (Raich and Nadelhoffer 1989) is based on the First Law of Thermodynamics (i.e., conservation of mass) and can be expressed as

$$\text{TRCA} \approx \text{soil respiration} - \text{litterfall} + \text{export} + \Delta C_{\text{root}} - \Delta C_{\text{soil}} \quad (1)$$

where units are grams of C per square meter per year and where soil respiration is CO_2-C released from the soil surface due to respiration by live roots and het-

erotrophs, litterfall is inputs to soil from aboveground production, export is C loss via erosion and leaching, ΔC_{root} is the change in root C (fine + coarse), and ΔC_{soil} is the change in soil C (forest floor plus mineral soil). The statistical model (same units) describes a simple linear regression that was derived from a collation of available data in which (export $+ \Delta C_{\text{root}} - \Delta C_{\text{soil}}$) was assumed to be small relative to C fluxes in litterfall and soil respiration. The published statistical model is

$$\text{TRCA} = 1.92 \times \text{litterfall} + 130. \quad (2)$$

This relationship suggests that C allocation to roots (for tissue production plus respiration) in forests increases with litterfall at the global scale.

The statistical model (Eq. 2) is useful for estimating C allocation to roots only when certain conditions are met (see Raich and Nadelhoffer 1989). First, reliable measurements of annual litterfall and soil respiration rates are required. These are relatively easily made, but details of the methods used must be evaluated in order to assess the quality of model inputs. Second, the model is applicable only in relatively mature forests with ". . . soils that are near steady state with respect to total organic carbon storage" (Raich and Nadelhoffer 1989: 1347). In other words, the terms "export," "ΔC_{root}," and "ΔC_{soil}" (Eq. 1) must be small relative to the other two terms in the conceptual model. Importantly, the model does not apply to young or to experimentally manipulated (e.g., fertilized, recently thinned) stands where C fluxes into and from soils can differ greatly and where changes in soil C pools can be large. We emphasize that soils should be *near,* but need not be *at,* steady state for application of the model. By stating otherwise, Gower et al. have misrepresented our model.

Criticism by Gower et al. of the use of C budgets is directed toward our published statistical relationship (Eq. 2) and focuses on three points: (1) the lack of a positive correlation between measured and predicted belowground C allocation; (2) the lack of a positive relationship between estimated fine-root production and predicted belowground C allocation; and (3) the potential misuse of our approach even if it is valid. Points (1) and (2) are legitimate attempts to invalidate the approach. Point (3) is misdirected in that the validity of the approach is questioned based on its potential for misuse. We respond below to each point.

Point 1.—The comparison between measured and predicted TRCA (Gower et al. 1996: Fig. 1) is not an appropriate test of our statistical model (Eq. 2) or of the overall C-budgeting approach because it is based on inappropriate data. Of the stands used in their com-

parison, only 3 of 17 were >30 yr old and were neither fertilized, irrigated, nor thinned (Gower et al. 1996: Table 1). Assuming that soil C content is near steady state in such stands is not realistic. Furthermore, methods used to estimate litterfall and soil respiration in 8 of their 17 stands are unpublished and therefore unverifiable. Data from four additional stands were not published as of November 1997 and data from two others were published in a non-refereed and unavailable symposium proceedings. Thus, methods for estimating litterfall and soil respiration were not specified for 16 of the 17 stands used in their comparison. Given the uncertainties and potential problems associated with methods for estimating soil C fluxes, the omission of information on methods underlying their results compromises their analysis.

Point 2.—The comparison between predicted TRCA and estimated fine-root production (FRP) made by Gower et al. (1996: Fig. 2) in which no correlation was found is specious because it assumes that FRP is measured accurately and equally well by a variety of methods. This assumption disregards an important body of research questioning the validity of models that use fine-root biomass measurements to estimate FRP (Singh et al. 1984, Lauenroth et al. 1986, Kurz and Kimmins 1987, Sala et al. 1988). It also ignores studies showing FRP estimates are strongly methods dependent (McClaugherty et al. 1982, Aber et al. 1985, Symbula and Day 1988, Nadelhoffer and Raich 1992, Sundarapandian and Swamy 1996). Gower et al. (1996) failed to mention that we previously reported a lack of correlation between FRP (as estimated by a variety of methods) and the predictor variable of TRCA (i.e., litterfall) at a global scale, "[f]or all data sets combined . . . there was no correlation between [fine-root production] estimates and litterfall" (Nadelhoffer and Raich 1992: 1142). The "test" of our statistical model as applied to temperate forests by Gower et al., therefore, was essentially the same relationship as we reported at a global scale (Nadelhoffer and Raich 1992: Fig. 1). In fact, values from 23 of the 34 temperate-forest stands used in Gower et al. (1996) were used in our previous analysis (Nadelhoffer and Raich 1992, with data from McGinty 1976, Harris et al. 1977, Grier et al. 1981, McClaugherty et al. 1982, Aber et al. 1985, Gholz et al. 1985, 1986, Nadelhoffer et al. 1985, Ellenberg et al. 1986, Joslin and Henderson 1987, Monk and Day 1988, Symbula and Day 1988, van Praag et al. 1988). The difference was that Gower et al. transformed litterfall (our independent variable) into predicted TRCA (their independent variable) prior to conducting their analysis. Furthermore, although Gower et al. (1996:1753) state that "There is . . . disagreement . . . as to the accuracy of various methods used to estimate belowground carbon dynamics," they focus pri-

marily on uncertainties associated with TRCA estimates and do not incorporate uncertainties in FRP estimates into their discussion. Instead, they use the lack of a significant correlation as an opportunity to speculate about possible factors that might cause patterns of aboveground and belowground C allocation by trees to vary from stand to stand. The likely possibility that methodological problems might compromise existing FRP estimates was omitted from their abstract in favor of this speculation.

Point 3.—Gower et al. (1996: 1750) express a well-founded concern that ". . . it may not be wise to use the [Raich-Nadelhoffer] model to estimate total root C allocation for specific stands where conditions may deviate significantly from the averages reflected in the data on which the model was based." However, the possibility that a technique or model may be misused does not serve to invalidate that technique or model. We agree that our model should not be used in situations where its underlying assumptions cannot be met. Unfortunately, these authors ignored their own dictum by applying our statistical relationship to a data set in which most of the stands were either aggrading (<30 yr old) or were recently thinned, irrigated, or fertilized. Soil C stocks in these stands were unlikely to be near steady state as the experimental manipulations likely altered primary production (C inputs to soils) and microbial activity (a major component of soil respiration). Therefore, a fundamental assumption of the model was violated in an attempt to test it. As such, their exercise fails to support the conclusion that our statistical model does not apply at less-than-global scales.

We agree with Gower et al. that site-specific measurements of TRCA (referred to as "TRCA-M" by these authors and based on Eq. 1) are superior to model-based predictions ("TRCA-RN," from Eq. 2). We did not suggest otherwise in either of our papers (Raich and Nadelhoffer 1989, Nadelhoffer and Raich 1992). Nor did we suggest, as implied by these authors, that litterfall alone may be used to define a soil C budget. We do maintain that until our statistical model is objectively invalidated, its use in generalized forest ecosystem models such as those of Aber and Federer (1992) and Ryan and Waring (1992) is justified.

Can carbon budgets be used to constrain fine root production estimates?

To illustrate how C budgets can be used to assess FRP estimates, we synthesize published values of C fluxes in a ~180-yr-old *Abies amabilis* stand described by Vogt et al. (1980, 1982) and Grier et al. (1981). At this site FRP was 554 g·m⁻²·yr⁻¹ (Gower et al. 1996, from Grier et al. [1981] and derived from sequential coring), litterfall was 106 g C·m⁻²·yr⁻¹ (from Grier et al. 1981), and soil respiration was 620 g C·m⁻²·yr⁻¹

(estimated from Vogt et al. 1980: Fig. 5). Therefore, the sum of C inputs from litterfall and estimated FRP (660 $g \cdot m^{-2} \cdot yr^{-1}$) exceeds measured soil respiration. This budget does not include the contribution to soil respiration from live-root respiration, which is at least equal to the C allocation to fine-root biomass (Mooney 1972, Penning de Vries 1975). Thus, a simplified soil C budget applied to this stand using on-site measurements of litterfall and soil respiration suggests that either the published estimate of FRP for this stand is unrealistically high or soil C accumulation was 600 $g \cdot m^{-2} \cdot yr^{-1}$, 5 times the measured C inputs via litterfall. We think the latter is unlikely and conclude that FRP at this site was greatly overestimated. We do not argue that the FRP estimate at this site is uniquely flawed. Rather, we use this extreme value (which, together with data from a younger *A. amabilis* stand located nearby the 180 yr-old stand contribute strongly to the negative correlation between FRP and model-based predictions of TRCA reported in Gower et al. [1996]) to illustrate problems inherent in estimating FRP using root-biomass measurements.

Summary and conclusions

Gower et al. (1996) provided no new insights into either the validity or the utility of the global-scale analysis of Raich and Nadelhoffer (1989). Gower et al. avoided addressing the use of soil C budgets to constrain estimates of fine-root production as proposed by Nadelhoffer and Raich (1992), and they presented no data showing that soil C budgets, *if used appropriately,* are unsuitable for use at stand, biome, or regional scales. Until better data become available, we must take advantage of existing information on forest C fluxes and recognize the fact that everything goes somewhere. Fluxes of C to roots that exceed annual C inputs to soils from aboveground sources by factors or ≥ 2 must be accounted for as increases in soil C or as measured losses (via respiration or other processes). We contend that statements such as ''76% of annual total net primary production by forests [may be] allocated to fine roots'' (Gower et al. 1996:1750) are insupportable unless the fate of such large allocations to roots can be accounted for in other ecosystem pools or fluxes.

The soil C-budgeting approach (Eq. 1) is one means of estimating total annual C fluxes to roots. It is based on the principal of conservation of mass and can be used to investigate belowground C fluxes in forests at local, regional, and global scales. Total C allocation to roots is estimated as the difference between C inputs via soil respiration in stands where C pools can be assumed as near steady state. When soil C is not near steady state, for example in aggrading or in recently disturbed forests, then additional terms (i.e., export,

ΔC_{root}, and ΔC_{soil} in Eq. 1) are required to reliably estimate belowground allocation using C budgets.

We concur with Gower and coauthors that the global-scale statistical relationship we derived using forest C budgets (Raich and Nadelhoffer 1989) should be evaluated at smaller scales. In our opinion, however, conclusions derived from our global-scale model, namely (a) that TRCA increases with aboveground net primary production (ANPP) and (b) that TRCA : ANPP decreases along global resource-availability gradients, form the basis of realistic working hypotheses about controls on root : shoot C allocation in mature, closed-canopy forests. Fair and objective evaluations of these conclusions using data from different sites than those used to develop the original model are clearly needed, as are continued efforts to identify how C-allocation patterns in forests vary in relation to stand age, species composition, and management practices.

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THE RELATIONSHIP BETWEEN LOCAL AND REGIONAL DIVERSITY: COMMENT

Mark Westoby[1]

Caley and Schluter (1997) compiled data on local vs. regional species richness, and arranged it following a graphical method proposed by Cornell (1985, 1993, Cornell and Lawton 1992). They concluded that local assemblages were not saturated with species. This comment argues that the procedure and reasoning they used has flaws, and should not be generally adopted. The comment is agnostic about the substantive issue of saturation, and addresses only the issue of how much weight should be given to the evidence presented by Caley and Schluter.

Inappropriate scale for "local" assemblages

Interest in testing whether local assemblages are saturated with species arises out of literature on species interactions within assemblages. The underlying idea is that a local assemblage is one where the component species are interspersed and interact with each other, affecting local persistence or extinction. The processes that might hypothetically cause saturation are interactions between species populations.

The smallest areas used by Caley and Schluter to represent local species richness were cells 50 × 50 km. (They also investigated cells 10 times that area, and regional species richness was counted in cells 500 × 500 km.) Of course it could be argued that the definition of "local" is just a matter of semantics. But in the context of discussions about species saturation, the point is that few would expect convergence of species richness due to within-community interactions to operate at a 50 × 50 km scale. To take land plants as an example, only small subsets of the species list in 50 × 50 km would occur as interspersed populations. Most species would be separated onto different landscape elements within the 50 × 50 km cell.

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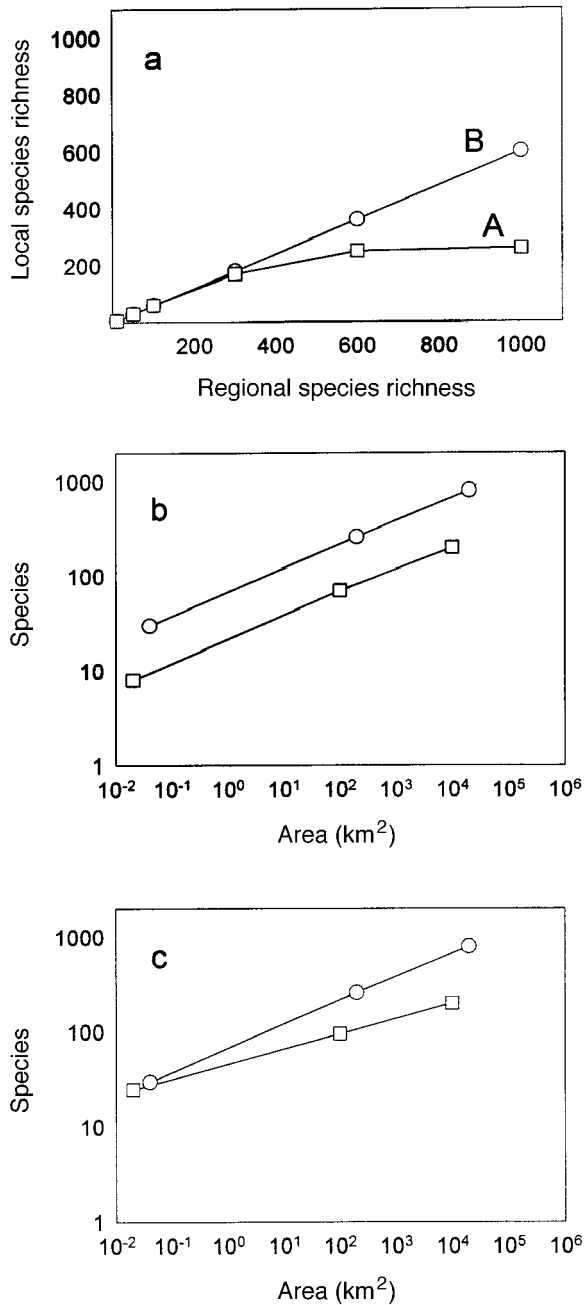
FIG. 1. Schematic graphs of species richness. (a) Local vs. regional species richness, after Cornell (1985, 1993) and Cornell and Lawton (1992). Data conforming to line A, which levels off, would indicate that beyond some point, further increases in regional richness produced no further increase in local richness, i.e., local assemblages were saturated. Data conforming to straight line B would indicate that extra species added to the regional richness also had some probability of increasing the size of the average local assemblage. The slope of line B quantifies this probability. (b and c) Species richness (log-scaled) vs. area (log-scaled), with separate relationships for each different continent or region being compared, after

Inappropriate combining of different groups of organisms

The purpose of graphing local vs. regional species richness is to detect leveling off in the relationship (Fig. 1a: line A). Leveling off would indicate that as one compares regions, moving from a smaller to a larger regional species list, local species richness does not continue to increase—in other words, local assemblages are saturated. Alternatively, if local species richness continued to increase progressively with the size of the regional species pool (Fig. 1a: line B), this would indicate absence of saturation. In Cornell's (1985: 1250: Fig. 1) original construction of such a graph, each data point was for the cynipine gall wasp assemblage on a single oak species. Regional gall richness varies among oak species, oaks with wider geographic distributions usually carrying larger regional gall faunas. These gall faunas on different oak species clearly have much natural history in common, and it was reasonable to hypothesize that local assemblages might saturate at the same level of species richness (Fig. 1a: A), or alternatively that local assemblages might be a consistent proportion of the regional fauna (Fig. 1a: B).

Caley and Schluter (1997: 74: Fig. 1) combined into a single graph data points from amphibians, birds, butterflies, corals, dragonflies, eucalypts, fish, mammals, reptiles, and trees, with separate data points from different continents where available. This graph showed no evidence of leveling off, and Caley and Schluter interpreted this as evidence against local (50 × 50 km) saturation. But surely there is no reason to expect any ceiling on local species richness to be set at the same level in such different groups of organisms. The slope of the linear relationship was ~0.6—in other words, 50 × 50 km species lists averaged around 60% of the 500 × 500 km species list. In Caley and Schluter's graph, moving from lower to higher regional species richness actually consisted of moving from fish, mammals, trees, etc. (regional richnesses all below 200) to birds (five data points for five continents, regional richnesses 200–800). If leveling off had been apparent, this would have meant that 50 × 50 km assemblages were a smaller proportion of regional assemblages for birds than for the other groups, rather than that there was a

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Westoby (1985, 1993); only two continents are shown for simplicity. Parallel relationships, as in (b), indicate that local assemblages do not converge in species richness between continents, but rather are proportionate to regional species richness. Diverging relationships, as in (c), indicate convergence of local species richness despite the difference in regional species richness.

ceiling on the species list of some particular type of 50 × 50 km local assemblage.

Cornell's formulation of plotting local vs. regional species richness (as in Fig. 1a) has very weak power when implemented for free-living organisms such as birds or trees, since at most there will be one data point (one level of regional species richness) per continent, unlike the situation for Cornell's gall wasps, where each host-plant species contributed a data point. Caley and Schluter's conclusions that local–regional slopes were uniform between taxa, and showed little evidence of curvilinearity, were founded on regressions using five data points for birds (Africa, Australia, Europe, North America, and South America), three for fish, three for mammals and four for reptiles. Regressions with this few data points have limited power to detect differences in slope, or curvilinearity.

An alternative formulation is to graph species richness for a given taxon against area (both log-scaled), with separate relationships for each continent or region (Fig. 1b and c). This formulation does not require arbitrary selection of two particular scales to represent ''local'' and ''regional,'' with data from regions that are to be compared needing to be exactly matched for scale. Parallel lines (Fig. 1b) indicate local assemblages are not convergent in species richness between different regions, but rather are proportionate to regional richness. When lines are close at local scales but diverge at wider scales (Fig. 1c), this indicates convergence in local species richness despite divergent regional richness.

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THE RELATIONSHIP BETWEEN LOCAL AND REGIONAL DIVERSITY: REPLY

M. Julian Caley[1] and Dolph Schluter[2]

In Caley and Schluter (1997) we addressed the relationship between local and regional diversity, specifically the issue of saturation of local species diversity. Westoby (1998) takes issue with several aspects of our analysis of saturation: (1) that the sizes of our local assemblages are too large to detect saturation; (2) that we inappropriately combined different groups of organisms in our tests; and (3) that an alternative method for detecting saturation based on species–area regressions is superior to our method, which used regressions of local on regional diversity. We dispute each of these claims as follows.

Appropriate locality size

If local species saturation occurs, then perhaps a correct locality size exists at which this saturation would be evident. Saturation may then not be detected if tested using larger or smaller localities, although this cannot be assumed a priori. The correct locality size is unknown, but it may be small, as Westoby suggests. However, a variety of tests has already been conducted using small localities, and little evidence for saturation has been found (references in Caley and Schluter [1997]). Our analyses explored instead the upper size limits of what might be considered a locality.

Our use of large localities was also meant to solve three less-well-appreciated problems. First, locality sizes used to study local–regional diversity relationships have varied depending on the taxon investigated, making intertaxon comparisons difficult. Second, tests of saturation must guard against ''pseudosaturation'' arising from sampling constraints in small localities. Most species are rare, and the reduced numbers of individuals associated with sampling a small locality means that fewer rare species will be included. Since

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more-diverse assemblages have more rare species than less-diverse assemblages, this sampling constraint will affect them more, causing ''local'' diversities to apparently converge between regions whose total diversities differ greatly. Our simulations revealed that the minimum sample sizes needed to avoid this artifact are surprisingly large even under ideal conditions in which every individual is sampled independently. The spatial dynamics of populations will usually prevent independence, necessitating even larger samples. Our use of larger-than-typical localities minimized the impact of pseudosaturation on our estimates of local–regional diversity relationships. Third, many prior studies have compared local diversity between regions that vary in size in order to include a wider range of regional diversities. However, variation in region size can bias estimates of local–regional relationships. To minimize this bias and to allow intertaxon comparisons, we used a consistent sampling protocol and a fixed region size, which allowed very broad comparisons among taxa and continents but made necessary a larger, and therefore, coarser ''locality.'' Our locality size is not ideal, as we stressed previously, but is informative and not otherwise inferior to smaller localities, which have their own limitations.

Combining taxa

We reported local–regional diversity relationships estimated from a wide range of taxa including amphibians ($n = 2$ taxa), birds ($n = 5$), butterflies ($n = 1$), corals ($n = 1$), dragonflies ($n = 1$), eucalypts ($n = 1$), freshwater fishes ($n = 3$), mammals ($n = 3$), reptiles ($n = 4$), and trees ($n = 2$) (Caley and Schluter 1997: *Appendix*). Increasing regional diversity was generally associated with a change in taxa, with mammals, reptiles, and freshwater fishes being the less diverse taxa and birds the most diverse. We agree with Westoby (1998) that ''there is no reason to expect any ceiling on local species richness to be set at the same level in such different groups of organisms,'' but we find the uniformity of slopes and the absence of any detectable curvature to these relationships intriguing. An asymptote in our across-taxon local–regional relationships could have occurred if the relationships for birds had been linear but shallower than less diverse taxa, or had been concave down. Alternatively, separate asymptotes for each taxon may have been obscured by combining taxa. These two possible outcomes might indeed engender different interpretations than we presented. Neither result, however, was evident in our survey. No slope differences among taxa were detected and no curvature was detected within intrataxon relationships for birds (locality = 1% of region, $P > 0.78$; locality = 10% of region, $P > 0.19$), the only taxon with sufficient data for such a test.

Tests of saturation

Westoby (1985, 1993, 1998) presents the species–area plot as an alternative to the local–regional plot for testing saturation. Species–area plots are illuminating but not superior to local–regional plots, which depict the actual saturation curve, and thereby visually aid intuition.

A drawback of the species–area approach is that the curve for each region requires several points, but tests of saturation that include multiple values of species richness from the same region will suffer from pseudoreplication. That is, the sample size for a test of saturation is the number of regions sampled, not the number of localities sampled within each region. Westoby's examples (1998: Fig. 1b and c) and his other applications of this approach (Westoby 1985, 1993) include only two or three regions, and are therefore insufficient for a test of saturation. Species–area plots, although not limited to comparing two regions, do not escape the problem that the earth presents very few biogeographic regions to work with.

A second potential problem with Westoby's examples is that they show convergence in species diversity at a locality size approaching 1 ha. However, 1 ha in the most species-rich region is unlikely to contain enough individuals of many multicellular taxa to avoid the problems of pseudosaturation discussed above. Surveys of large-bodied taxa, such as most of those in our survey, require either corrections for pseudosaturation or much larger localities.

Conclusions

Perhaps there exists an appropriate locality size for each taxon at which saturation is evident, and where this saturation becomes blurred when surveys are conducted using smaller or larger localities. However, a growing number of local–regional comparisons at a range of scales along the locality-size spectrum, from a single oak tree (Cornell 1985a, b) to 25 000 km^2 areas on a map (Caley and Schluter 1997) suggests that local saturation is elusive. Many processes can result in the number of species coexisting within any locality of arbitrary size being determined to a considerable extent by inputs from the surrounding region, and therefore will be determined in part by the diversity of that region. Absence of saturation does not imply local processes have no impact on the character of local species assemblages—only that such processes place no hard limits on the numbers of species that may coexist locally. Our results and those of others suggest that regional effects are strong. Understanding the diversity of local assemblages requires that regional processes be considered.

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HOW RISKY IS BIOLOGICAL CONTROL? COMMENT

J. H. Frank[1]

The authors of a paper "How risky is biological control?" (Simberloff and Stiling 1996) wrote about the risk of dispersal of biological control agents to areas that were not intended to be occupied, and to nontarget species. They claim that introduction of biological control agents is risky, and that such agents should be judged "guilty until proven innocent." I think the legal metaphor chosen by Simberloff and Stiling is inappropriate, and I prefer to compare biological control to surgery rather than to law. First, as in biological control, surgery is one of several alternative courses of action to address a specific problem. There are risks

associated with surgery and with alternatives to surgery, and these must be compared. Second, as in biological control, surgery has advanced in the past 130 years. It is no more appropriate to criticize modern biological control for disastrous introductions of the distant past (e.g., of the Indian mongoose, *Herpestes auropunctatus*) than to criticize modern surgery for deaths through lack of antiseptic methods used in the past, but many have learned from such errors.

I agree with Simberloff and Stiling that risk/benefit analysis is an important preliminary to biological control introductions. As an example of an introduction of biological control agents against nonindigenous pest insects, Simberloff and Stiling cited actions of the University of Florida's mole cricket research program. In this comment I provide a risk/benefit analysis of introductions made by this program. Because I have been involved in the program for 12 years I am familiar with data (published only recently hence less readily available to Simberloff and Stiling) relevant to the questions posed by Simberloff and Stiling. They ask: "What is the likelihood that these [introduced] control agents would spread and, if they did, what is the probable effect on [a] native species [of mole cricket, *Gryllotalpa major*]"? I ask, additionally, what are the likely environmental and economic effects of alternatives to introducing these biological control agents? My goal in this comment is twofold. First, I show how ecologists knowledgeable of a biological control system can conduct necessary risk/benefit analyses. Second, I show that in the specific case of mole cricket biological control the risks to *G. major* are trivial, but that the cost (to agriculture and horticulture) of not undertaking the program is very high and the harm from currently used chemical pesticides to nontarget organisms is widespread.

A broad perspective of biological control

From January 1971 to late 1991 (a period of not quite 21 years), 271 immigrant insect species were newly reported as established in Florida (Frank and McCoy 1992). Few of these uninvited species have been studied. Among the immigrants were a few species, on average detected at about one per year, that either were known to be important pests elsewhere, or made their presence conspicuous as major pests (Frank and McCoy 1992). When these pests affected agriculture in the broadest sense, or infested buildings, or caused annoyance by biting, they became targets of control by repeated application of existing broad-spectrum pesticides. The natural trend is therefore for increasing use of pesticides, which is beneficial for commerce and creates jobs, but is costly to purchasers and detrimental to the environment. These invasive species may thus have far greater effects on ecosystems, both directly

and indirectly by prompting use of chemicals, than do the few specialized biological control agents that were imported and established during this period (Frank and McCoy 1993) to reduce pest populations.

Sometimes exotic pests proved very costly to control by chemicals or proved not very susceptible to existing chemicals, and these were the first to be evaluated for possible biological control. In other words, it is generally the failure of chemical control that instigates a biological control campaign. This reflects economic pressure rather than environmental benefit, but it is economic pressure that most often generates research funds for biological control. Biological control campaigns are also occasionally initiated against immigrant pests of native plants with no assigned commercial value, with no motive other than to protect the environment (e.g., Frank and Thomas 1994), but funding for such campaigns is abysmally difficult to obtain.

Simberloff and Stiling advocate that biological control agents should be tested against nontarget organisms before release. They suggest that even if a biological control agent does not now attack a nontarget organism, it may later evolve to do so. I think that biological control agents should be tested against nontarget organisms that are closely related to the target pest. I also think that environmental and economic costs of inaction and of alternative actions should be weighed.

In the example of the introduction of three biological control agents against *Scapteriscus* mole crickets in Florida, no testing against the rare *Gryllotalpa major* was performed because of allopatry and distant relationship of *G. major* to *Scapteriscus.* Native congeners of the biological control agents had failed to attack the invading *Scapteriscus* mole crickets in an inadvertent field experiment of ≥80 yr, suggesting that a rapid host shift by the biological control agents would not occur. Large economic losses caused by *Scapteriscus* mole crickets, and harm done by chemical pesticides to nontarget organisms, ruled against a long-term test for a host shift before release. Subsequent data have thus far vindicated the risk that was taken and have shown benefits from the releases. No risk/benefit analysis was written before release because none was then required (only a statement of host specificity was required), but requirements for documentation are now more stringent in permit applications.

Phylogeny and biogeography of mole crickets

The pest mole crickets in the southern USA are three South American species of *Scapteriscus* which arrived in ships' ballast ~1900. These belong to the tribe Scapteriscini, whereas native mole crickets belong to the genera *Neocurtilla* and *Gryllotalpa* of the tribe Gryllotalpini (Otte 1994) and differ in behavior, habitat, physiology, and natural enemies. The invading *Scap-*

teriscus species have colonized sandy and otherwise friable soils of the coastal plain in the subtropical and mild temperate climatic zones of the southern USA plus, recently, the southern Arizona–California border (Frank 1994).

Of the two native mole crickets considered by Simberloff and Stiling, *Neocurtilla hexadactyla,* occurs in heavy soils in the eastern USA northward to the Great Lakes. It never was a target of biological control, and is not rare (Frank 1994). I use this species, because it is native in the areas where the biological control agents were released and because the mole cricket program has data about it, as a model for the tribe Gryllotalpini. Simberloff and Stiling express concern about *Gryllotalpa major,* which occurs in heavy soils in prairie remnants in Arkansas, Kansas, Missouri, and Oklahoma and is rare because of habitat loss (Vaughn et al. 1993). It was proposed in 1990 as a candidate for federal listing as a threatened species (not as an endangered species, as stated by Simberloff and Stiling), but was removed from candidacy in 1992 because it is not as rare as had been suspected (Vaughn et al. 1993).

Specificity of native natural enemies

The native *Neocurtilla hexadactyla* has its own specialized natural enemies including the wasp *Larra analis* (Sphecidae) and the nematode *Steinernema neocurtillae* (Steinernematidae). Six native species of flies of the genus *Ormia* (Tachinidae) are parasitoids of various insects (some Orthoptera, some unknown), but none of their hosts is a mole cricket.

Simberloff and Stiling, reasonably, express no concern about *N. hexadactyla,* which has somehow expanded its range to South America and has even been considered a pest there (I presume that its native North American natural enemies did not accompany it to South America). They express concern for *Gryllotalpa major,* which is far more closely related to *N. hexadactyla* than to *Scapteriscus.* No specialized natural enemies of *G. major* are known.

Introduced biological control agents and the risks they pose

The targets of the mole cricket program are the three *Scapteriscus* species, which differ considerably from one another in behavior and susceptibility to the introduced biological control agents (Frank 1994). Just as *N. hexadactyla* has its own specialized native natural enemies in the USA, so *Scapteriscus* spp. have specialized natural enemies in South America. Those that the mole cricket program has imported, released, and established in Florida against *Scapteriscus* are *Larra bicolor, Ormia depleta,* and *Steinernema scapterisci* (Frank 1994).

Larra spp. are diurnal digger wasps for which the

only recorded hosts are mole crickets (Menke 1992). The only *Larra* species imported from South America and established in Florida is *Larra bicolor,* first from a stock originating from Belem, Pará, Brazil (via Puerto Rico), and later from a stock from Santa Cruz, Bolivia (Frank et al. 1995). The Brazilian stock of *L. bicolor,* apparently for climatic reasons, failed to become established in central and north Florida, despite releases there. The Bolivian stock became established at 29° N, its only place of release. This *Larra* species is a specialist on *Scapteriscus* mole crickets and is normally repelled by the defensive behavior of *Neocurtilla hexadactyla* (Castner 1984). Under laboratory conditions, when *N. hexadactyla* and a female *L. bicolor* are confined together in a glass vial, the attacking female *L. bicolor* sometimes succeeds in laying an egg on *N. hexadactyla,* but the resultant *Larra* larva dies, apparently due to physiological defenses of this nonhost mole cricket (Pruett and Bennett 1991). Evidence of specialization also comes from early attempts at introduction of *L. bicolor* into Hawaii in the 1920s against a nonindigenous *Gryllotalpa* species; the wasp failed to become established (Frank et al. 1995). The biological control practitioners at that early date failed to understand that *L. bicolor* specializes on *Scapteriscus* mole crickets, and that *Scapteriscus* is not closely related to *Gryllotalpa.* These observations suggest that a host shift by *L. bicolor* to mole crickets of the tribe Gryllotalpini is a remote possibility.

Ormia spp. females are nocturnal, larviparous, phonotactic flies that locate hosts (from some distance) by tracking the courtship song of male hosts (e.g., Robert et al. 1992). The stock of *Ormia depleta* imported into Florida is from Piracicaba, São Paulo, Brazil. Releases were made in all regions of Florida (and in Alabama, Georgia, and North Carolina), and the fly has occupied all areas south of ~28° N, but has not achieved a permanent presence northward (Frank et al. 1996, Walker et al. 1996). Evidence for its specificity to *Scapteriscus borellii* and *S. vicinus* is given by Frank et al. (1996). The songs of its *Scapteriscus* hosts are continuous trills, whereas that of *G. major* is a set of brief chirps, resembling that of the nonhost *N. hexadactyla* (Walker and Figg 1990). Since its introduction, *O. depleta* has not adapted to attack *N. hexadactyla* (we have found no infected specimens), which is not rare and is now sympatric with *Scapteriscus* in the coastal plains. The available data suggest a host shift to *Gryllotalpa* or *Neocurtilla* is unlikely.

Steinernema spp. are entomopathogenic nematodes with considerable interspecific differences in specialization to hosts. In the early 1980s some 2000 mole crickets trapped at various locations in Florida were held for emergence of entomopathogenic nematodes. Some *Neocurtilla hexadactyla* produced a steinerne-

matid nematode described later as *Steinernema neocurtillae,* which has not yet been found in any other mole cricket (Nguyen and Smart 1992). Trapping of *Scapteriscus* mole crickets in Uruguay, however, yielded a steinernematid nematode subsequently described as *Steinernema scapterisci* which proved to be highly pathogenic to *Scapteriscus borellii* and *S. vicinus,* but not to *S. abbreviatus* even under ideal laboratory conditions (Nguyen and Smart 1991). Establishment was obtained in small plots in Florida pastures in 1985. These plots were monitored weekly for five years by trapping mole crickets, holding the mole crickets individually in vials, and identifying nematodes that emerged from all dead and dying mole crickets. Some 200 *N. hexadactyla* were trapped, along with many more *Scapteriscus* spp., but only *Scapteriscus* spp. were infected by *S. scapterisci* (Parkman et al. 1993). There is thus no evidence that *S. scapterisci* attacks *Neocurtilla hexadactyla* even when the latter exists commingled with an infected *Scapteriscus* population in Florida. That *N. hexadactyla* has its own entomopathogenic nematode, *Steinernema neocurtillae,* which has not been found in *Scapteriscus,* suggests that these two nematode species are coevolved with their hosts and that transfer to mole cricket hosts of other tribes is very improbable.

The main use of steinernematid nematodes has not been as classical biological control agents (as above), but as biopesticides, to be applied at very high density ($\sim$200 000/m^2) to soils in expectation of immediate kill of target pests whose defenses are overwhelmed by huge numbers of the nematodes. Biossays of several nematode species (e.g., Ricci et al. 1996) show poor performance of *S. scapterisci* in standardized tests against larvae of wax moth (*Galleria mellonella*), indicating that it would not be an effective biopesticide for general use. However, *S. scapterisci* makes a good biopesticide for use against *Scapteriscus borellii* and *S. vicinus,* achieving kill of these insects comparable to that achieved by chemicals. This nematode is produced and marketed for that purpose alone in the coastal plains of the southern USA. A recent intensive review of the use of steinernematid and heterorhabditid nematodes as biopesticides demonstrated them to be relatively safe to nontarget organisms (Bathon 1996, Ehlers and Hokkanen 1996, Parkman and Smart 1996, and others in the same volume).

Climate and allopatry reduce risks

These three introduced biological control agents originated from the tropical (*Larra bicolor, Ormia depleta*), and mild temperate regions (*Steinernema scapterisci*) of South America. These organisms were released in Florida without knowledge of the northernmost latitude they might occupy in the continental

USA, because it cannot be predicted accurately. The hope was that they might occupy the entire range of North America that is now occupied by invasive *Scapteriscus* mole crickets: the milder climates of the coastal plains from North Carolina to Florida and west to Texas (not including the prairie states). Reality shows that the Belem strain of *Larra bicolor* has been unable to survive north of southern Florida, and the Santa Cruz strain occurs only at 29° N in northern Florida. I expect that *L. bicolor*'s range will expand southward, but I am no longer optimistic that it will expand northward because of its tropical origin. The Piracicaba strain of *Ormia depleta* has not been able to establish a permanent presence even as far north as 29° N. Of the three biological control agents that the mole cricket program has established in Florida, *Steinernema scapterisci* is the most likely to be able to tolerate the winter temperatures of the states in which *G. major* exists, because this species occurs naturally at 35° S in *Scapteriscus borellii* in the pampas of Argentina (Stock 1995). However, the imported stock came from Uruguay and has not yet been shown to survive the winters north of ~31.5° N (southern Georgia) although it has been tested and marketed as a biopesticide in South Carolina (C. Gorsuch, *unpublished data*). Simberloff and Stiling express concern that one or more of these three biological control agents might attack *G. major* in Arkansas, Kansas, Missouri, or Oklahoma (33°–40.5° N). Current evidence of climatic limitations of the imported stock of biological control agents suggests that such a range expansion is unlikely.

The range of *G. major* is distant from that of any of the *Scapteriscus* invaders in the USA. For propagules of any of these biological control agents to cross hundreds of kilometers of territory unoccupied by mole crickets other than *N. hexadactyla* (which proves not to be a suitable host for any of them) and then instantaneously (death is at most weeks away) to adapt to a scarce nonhost (*Gryllotalpa major*) that is much more closely related to *N. hexadactyla* than to the *Scapteriscus* hosts is so remote as to be untenable.

Evolution of natural enemies, and rarity of G. major

If the imported biological control agents are to evolve to kill *G. major,* then the possible steps are: (1) evolve to kill and reproduce in *N. hexadactyla,* (2) adapt to colder climates, (3) expand range using *N. hexadactyla* as hosts until sympatry with *G. major* is achieved, and (4) evolve to kill yet another host, *G. major*. An alternative scenario is that (1) one of the *Scapteriscus* species (most likely *S. borellii*) expands its range to become sympatric with *G. major,* (2) that one of the biological control agents adapts to colder climates and follows this host, and (3) that this biological control agent evolves to kill *G. major*. I cannot state categorically that these steps will never happen, nor can I state that some hummingbird will never evolve to insectivory, but I think the risks are extremely low. The results of a (now) >90 yr inadvertent field experiment have, after all, failed to show the possibility of one of the steps: host-switching by native natural enemies belonging to the genera *Larra, Ormia,* and *Steinernema* to invasive *Scapteriscus* species, despite the abundant food supply represented by these pest mole crickets.

The rarity of *G. major* provides a safeguard. If, somehow, one of the imported biological control agents arrives in the habitat of *G. major,* the frequency of encounter with this mole cricket would be low and this would hinder a host shift.

The risks of alternatives to biological control

Simberloff and Stiling question the risks of introducing the three above-mentioned biological control agents. The other side of the balance sheet is the benefit that biological control of *Scapteriscus* mole crickets can achieve. At stake, in Florida alone (much more is at risk in other southern states) are ~10^6 ha of bahiagrass (*Paspalum notatum*) pastures, ~5×10^5 ha of bahiagrass and bermudagrass (*Cynodon* spp.) turf (including ~1200 golf courses), other pasture and turf grasses, and ~45 000 ha of the most susceptible vegetables (tomato, bell pepper, egg plant, cabbage, and cucurbits).

Bahiagrass pastures are the mainstay of beef- and dairy-cattle production in Florida and are damaged by *Scapteriscus* mole crickets to the point that pastures may be entirely destroyed. The only alternatives to the biological control agents that the mole cricket program has introduced are (1) no action, and (2) a few chemical pesticides that can be used where cattle graze. Frequent use of those pesticides is too costly for most cattle ranchers because of the low prices for beef, and in the past they have used the cheap but persistent and environmentally harmful pesticide chlordane (Frank 1994).

In 1986, damage and costs of control to turf grasses by *Scapteriscus* mole crickets in Florida were estimated as >$44 million annually, with an additional $33 million in Alabama, Georgia, and South Carolina; losses in other states (North Carolina, Louisiana, Mississippi, and Texas) were not estimated (R. D. Hudson, *unpublished presentation*). As a result of the damage they cause in the southeast, *Scapteriscus* mole crickets are the most important pests on golf courses in the country (Shaw 1993). The standard method of treatment in Florida as in other southern states is the use of broad-spectrum chemical pesticides (e.g., carbaryl, ethoprop, and fonofos). Playing fields and home lawns are extremely important sites of use of chemical pesticides

in Florida, with expenditures on control of *Scapteriscus* unrelated to economic returns and very high because of Florida's large human population, expectation of year-round use of turf, and mild climate. Roadside rights-of-way are often damaged by mole crickets, and Department of Transportation personnel want alternatives to chemical pesticides. The reality of massive kills of birds after ingesting diazinon-poisoned mole crickets on golf courses ended in 1988 (the year that the mole cricket program released its third biological control agent in Florida), and only the specter seems to remain (Rainwater et al. 1995). Yet, an equal reality is that harm to nontarget invertebrates has hardly lessened. Chemical insecticides such as ethoprop, carbaryl, and fonofos at labelled dosages are lethal to earthworms, and other chemical pesticides that are commonly used against mole crickets suppress populations of nontarget arthropods such as spiders, carabids, and staphylinids that can serve as generalist predators of mole crickets (Potter 1994 and references therein). Populations of many hundreds of nontarget invertebrate species are harmed on golf courses and lawns and playing fields in the southern USA by treatment with chemical pesticides against *Scapteriscus* mole crickets. Unfortunately, nobody has assessed the value of such invertebrates.

Now, vegetable fields in Florida are usually fumigated with a methyl bromide/chloropicrin mixture to control soil-dwelling pests including mole crickets (e.g., Noling and Becker 1994). This chemical mixture is a potent biocide which kills virtually all soil organisms.

The picture, though economists have documented little of it, is one of tremendous annual losses due to *Scapteriscus* mole crickets, with chemical pesticides still the overwhelming recourse for preventive use by farmers, ranchers, and turf managers. Biopesticides like *Steinernema scapterisci* (and also *S. riobravis,* a less specialized nematode from the southwestern USA) currently make up a tiny percentage of total use. Classical biological control agents (*Larra bicolor, Ormia depleta,* and *Steinernema scapterisci*) are reducing populations of *Scapteriscus borellii* and *S. vicinus* (Parkman et al. 1996; H. Frank *unpublished data* for 1995–1996) and are therefore reducing the need to apply pesticides. However, their contribution is little appreciated, because nobody outside the mole cricket program even monitors their presence, much less their effects on mole crickets. Tens of millions of dollars worth of chemical pesticides are applied annually to soils in Florida (and much more in other southern states) to kill *Scapteriscus* mole crickets, and such applications yield only temporary control. The chemicals do not kill *Scapteriscus* mole crickets only, and it is likely that most soil-dwelling invertebrates are killed by chemical pesticides over hundreds of thousands of

hectares annually. Annual sales of chemicals for control of *Scapteriscus* mole crickets are an important source of revenue for chemical companies which, naturally, do not support the development of biological control alternatives.

Scapteriscus mole cricket populations vary in time and space and therefore so does the damage they cause and the cost of chemicals used against them. Incomplete economic data exist for mole crickets in turf, not in pastures or vegetables. Such data do not address the question of the damage done by chemical pesticides to nontarget invertebrates.

The surgery performed by introduction of biological control agents against *Scapteriscus* mole crickets is justified environmentally and economically. It has not caused collateral damage and appears unlikely to be able to do so.

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HOW RISKY IS BIOLOGICAL CONTROL? REPLY

Daniel Simberloff[1] and Peter Stiling[2]

If a surgical rather than a legal metaphor is appropriate for biological control (Frank 1998), we cannot agree that, because biological control, like surgery, has learned from errors in the past, all current practices are beyond criticism. For example, the recent introduction of the flatworm *Platydemus manokwari* to several islands in the Pacific and Indian Oceans (e.g., Muniappan 1987) to control the giant African snail (*Achatina fulica*) is widely seen as potentially as damaging to nontarget native species as that of the small Indian mongoose (*Herpestes auropunctatus*) that Frank concedes was disastrous. This project seems not to have been informed by the well publicized global extinctions of native snails caused by earlier introductions to control the giant African snail (Hopper and Smith 1992); the wide introduction of a generalized predator is the antithesis of surgical. Of course much of modern biological control, particularly of plants, is practiced with more concern than in the past about potential impacts on nontarget species. However, potential risks, costs, and benefits are still not carefully analyzed in many projects. Our paper (Simberloff and Stiling 1996) sought to demonstrate this problem and to point out that such analyses will not be easy. Frank's attempts along these lines are certainly a beginning, but many weaknesses remain.

For risk, he argues that, since native congeners of introduced biocontrol agents have failed to attack *Scapteriscus* mole crickets in 80 years, there is little reason to believe that the introduced species themselves would attack native hosts. We are unaware of any basis for this reasoning. Granted that the probability of a rapid host-shift by any host-specific species is probably low, we know of no literature that suggests that, if species *A* has not shifted hosts in time interval *X,* congeneric species *B* is unlikely to shift hosts in time interval *Y.* Certainly there is need for much research on this point. It is known that rapid host shifts do occur (see, e.g.,

Dennill et al. 1993, Secord and Kareiva 1996), but the circumstances that promote such events in nature have barely been studied. The trajectory of one introduced species often gives little information about the likely trajectory of a closely related species (Williamson 1996).

As further evidence that a host shift is exceedingly unlikely for *Larra bicolor,* Frank points out that attempts to introduce it into Hawaii in the 1920s against a nonindigenous *Gryllotalpa* species failed. His interpretation is that this failure shows that *L. bicolor* is unlikely to shift to hosts in the tribe Gryllotalpini. The relevance of these failed introductions of *L. bicolor* can be questioned. First, how do we know the failure to establish was due to absence of a suitable host? The invasion literature, including that on biological control, has numerous examples in which several introductions failed and eventually one, apparently of an identical propagule, succeeded. A classic example is that of the introduction of the House Sparrow (*Passer domesticus*) to North America (Long 1981). An initial propagule of 16 birds failed in 1851, as did a second one a year later, in the same place, of ~50 individuals. A third release the next year in the same place, again of ~50 individuals, survived and spread; this species is now one of the most numerous in North America. The coreid bug *Chelinidea vittiger* was liberated on Santa Cruz Island (California) in 1945 for control of prickly pear (*Opuntia* spp.), but failed to establish; however, at least one of four releases on the same island in 1961–1964 was successful (Goeden 1977). Although differences in propagule size and genetics often complicate such cases, a common interpretation of this situation is that the failures were due to demographic stochasticity (Williamson 1996). In any event, because *L. bicolor* never established in Hawaii in the 1920s, it is difficult to see how this case can tell us much about its likelihood of shifting hosts where it *has* established.

As a final comment on Frank's assessment of risk, of course we concede that the probability that any of these biological control agents for mole crickets can cross hundreds of kilometers on their own to reach the range of *G. major* is low. How low is uncertain; species do occasionally make very difficult voyages autonomously. For example, the cactus moth *Cactoblastis cactorum* managed to spread on its own from Hawaii to all the other major Hawaiian islands (Tuduri et al. 1971) in just seven years. Further, many species can hitchhike. Pemberton (1995) argues that *C. cactorum* got part way from the Lesser Antilles to the Florida Keys, where it is devastating a candidate endangered species of *Opuntia,* by air transport of plants from the Greater Antilles to Miami. Turf and sod are carried on trucks; what is the probability that mole cricket natural enemies could move this way?

We do not wish to belabor the point that any of these scenarios carries a low probability. What is important is that events of low probability do happen, they have to be analyzed more quantitatively than in the past, and such analysis will not be easy. Frank has simply stated some of the factors that have to be taken into account.

Frank's analysis of costs and benefits is also very incomplete, at least partly because crucial data are simply unavailable. As is typical for claims of tremendous economic benefits of biological control, the only basis for estimating the cost of mole cricket impact on turfgrasses is an unpublished document, this time a handout at a 1986 meeting of the Georgia Entomological Society (R. D. Hudson, *unpublished presentation,* cited by Frank [1998]). Frank concedes that ''economists have documented little'' of the ''tremendous annual losses due to *Scapteriscus* mole crickets,'' and also that nobody has assessed the value of nontarget invertebrates. Thus we are left with a list of some of the crops that these mole crickets damage and no way to assess the full costs, current or possible, of alternatives to attempt to control the mole crickets. We also observe that Frank assumes there are just two possible alternatives for dealing with these mole crickets: classical biological control and broad-spectrum pesticides. At least for some pests, one can imagine other possibilities (see, e.g., U.S. Congress 1995).

In sum, biological control is not always practiced today with surgical precision, and risks, costs, and benefits are rarely comprehensively analyzed. We do not claim that the introductions made by the mole cricket research program that Frank defends have been or are likely to be damaging. However, we do not believe that Frank has settled this matter or that he has pointed the way to an adequate analysis of costs and benefits of various courses of action. We note that this exchange of views is relevant to many cases aside from this particular program. It is eerily similar to the defense of musk thistle (*Carduus nutans*) biocontrol by P. E. Boldt (*unpublished letter*) and the response by S. M. Louda et al. (*unpublished letter*). The conflict between practitioners and critics of biological control does not seem near to resolution.

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ECOLOGICAL CORRELATES OF REGIONAL VARIATION IN LIFE HISTORY OF THE MOOSE ALCES ALCES: *COMMENT*

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Sæther et al. (1996) compared some life-history characteristics of four Norwegian moose (*Alces alces*) populations occupying ranges of varying quality to test the food-limitation hypothesis and concluded (p. 1499)

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that ''a stable high-density equilibrium between moose and their food resources is unlikely to occur.'' However, their data set may not justify such a conclusion because they neglected to consider the role of a major component in the dynamics of the moose populations studied: human harvests. On the basis of the simple models proposed by Caughley (1976) for plant–herbivore interactions and regulation of large-ungulate populations, Sæther et al. (1996) cannot use population dynamics of moose in Norway to reject the hypothesis of regulation by competition for food.

To alleviate any semantic confusion, it is worth defining four concepts that are central to the understanding of Caughley's (1976) approach to population dynamics of large herbivores: K carrying capacity (KCC; Macnab 1985), limiting factors, regulating factors (Messier 1991) and sustained yield (SY). KCC represents ''the equilibrium reached between herbivores and their food supply'' after dampened oscillations (Macnab 1985:404). Limiting factors refer to ''any processes that quantifiably affect population growth and are responsible for year-to-year changes in the rate of population growth'' (Messier 1991:378). Regulating factors designate ''any density-dependent processes that ultimately keep populations within normal density ranges'' (Messier 1991:378). Thus regulating factors represent a subset of limiting factors, characterized by negative-feedback mechanisms that depress population growth as animal abundance increases. Finally, SY equals the annual surplus of births over deaths observed when an ungulate population below KCC is increasing; if these animals are harvested, the population remains stable below KCC.

Sinclair and Arcese (1995) described three alternative hypotheses related to regulation of large herbivores: the predator-regulation hypothesis, the predation-sensitive food hypothesis, and the surplus (or food-limitation) hypothesis. In the first case, density-dependent predation causes herbivores to stabilize at low density (relative to KCC) with access to ample quality forage. Moose populations preyed upon by wolves (*Canis lupus*) and black or brown bears (*Ursus americanus, U. arctos*) support this hypothesis (Messier and Crête 1985, Crête 1987, Gasaway et al. 1992). According to the second hypothesis, herbivore numbers stabilize at a density lower than KCC because predators remove some vulnerable herbivores that would otherwise survive. This model might apply to Isle Royale moose where only wolves prey on moose (McLaren and Peterson 1994). In the third case, the food-limitation hypothesis supposes that competition for forage causes density to stabilize at KCC, predators having no influence on herbivore density. This hypothesis

should apply to Fennoscandian moose because wolves and brown bears have been reduced to insignificant numbers during the current century (Cederlund and Markgren 1987). Given the food-limitation hypothesis, one should still expect density to fluctuate around KCC, as observed for moose on Isle Royale (McLaren and Peterson 1994) or wildebeest (*Connochaetes taurinus*) in the Serengeti (Sinclair and Arcese 1995), due to the combined effects of limiting factors (e.g., winter harshness) and forest dynamics (e.g., forest fires).

In order to test the food-limitation hypothesis of population regulation, Sæther et al. (1996) had to study moose populations in the proximity of KCC because, in large mammals, regulation generally operates at densities approaching KCC (Fowler 1981). However they provided no figures on either absolute moose density, or density with respect to KCC. Crête (1989) estimated KCC in an area of deep snow of eastern Quebec to exceed 2 moose/km^2; the estimate varied between 3.6 and 6 animals/km^2 in southwestern Quebec due to greater forage production. Very few data have been published on Fennoscandian moose density, and none to my knowledge for unharvested populations. Bergström and Vikberg (1992) reported that the density increased from 1.3 to 5.7 moose/km^2 in a forested enclosure of central Sweden before being reduced by hunting. Most likely, KCC must approach 10 animals/km^2 in very productive areas of Fennoscandia, particularly because of the limited snow cover (Sæther et al. 1996).

The four moose populations studied were harvested annually at a rate of 0.33–0.50 animal/km^2 (Hjeljord et al. 1994). With the information provided, it is impossible to compute which proportion of the population this SY represented, but such yields are comparatively high (Crête 1987). Most likely, annual harvests have kept densities much below KCC, particularly for the Alpine population that occupied a poor range (Sæther et al. 1996). Not surprisingly, Sæther et al. (1996) found no evidence of regulation driven by competition for forage.

However, Sæther et al. (1996) found that winter climate was a limiting factor for their moose populations, as calf mass increased by $\cong 40\%$ during two snow-free winters (a very unusual situation for moose [Bédard et al. 1974]), and larger body size after mild winters resulted in higher fecundity of yearling females. From this observation, they concluded that regulating factors due to competition for forage likely contributed less to variation in recruitment rate than variation due to climate. Sæther (1985) had already identified summer climate as a limiting factor for moose in Norway, its influence on somatic growth differing however between the south and the north of the country. Sand et al.

(1995) observed that climatic harshness influenced body mass of adult Swedish moose more than density or browse availability, whereas Crête and Courtois (1997) found a relationship between winter and summer climate and calf production in an unproductive boreal range of northeastern Quebec. As Sæther et al. (1996) observed in Norway, Sand (1996) also noted that the relationship between body mass and sexual maturity varied with latitude for Swedish moose. Three conclusions can be drawn from the preceding observations: (1) Sæther et al. (1996) could not compare the relative importance of climate and competition for forage for moose fecundity because they had no data for populations regulated by food. (2) Climate might play a minor role in moose demography if influencing only somatic growth and sexual maturity; adult fecundity and survival have greater effects on population growth of cervids than sub-adult fecundity (Nelson and Peak 1982, Crête et al. 1996). (3) Climatic factors exert a variable influence on population dynamics throughout the range of moose. In this respect, the idea first proposed by Haldane (1956) could be true for moose—that regulation might be easier to detect in the core of the species range whereas limiting factors might gain in importance at the periphery (Crête and Courtois 1997).

Sinclair (1991) advocated the utilization of control and manipulated animal populations through wildlife management for scientific experimentation. In order to test the existence of density-dependent regulation by competition for forage in Fennoscandian moose and to test the stability of the equilibrium, one should exclude moose from hunting over an area large enough (~ 1000 km^2) to reduce the importance of emigration (Crête 1989) and should monitor major demographic variables for comparison with contiguous, harvested populations. Doing the study in the core of the range of moose might yield more conclusive results than at the periphery.

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ECOLOGICAL CORRELATES OF REGIONAL VARIATION IN LIFE HISTORY OF THE MOOSE ALCES ALCES: *REPLY*

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In a comment about Sæther et al. (1996), Crête (1998) questions our conclusion that a stable high-density equilibrium is unlikely to exist between moose and food in the absence of predation by large carnivores. According to Crête, our conclusion is unjustified because we did not present any data on the density of the moose populations in our study areas.

The basis for the criticism by Crête is a failure to realize the difference between an individual-based and a population-level approach to questions in population ecology. A necessary condition for population regulation through food limitation is that a negative feedback exists between the population growth rate and population density (Turchin 1995). This implies that, at the individual level, the probability of survival and/or the number of offspring produced should decrease when the food supply is decreased. Our approach was therefore to measure food intake during the season when access to food was assumed to be most critical in populations with great differences in food supply, and to relate such differences in intake to demographic variation. No evidence was found that variation in mortality was related to food intake rate in winter. The only demographic change that occurred was a reduction in fecundity on the very poor winter range in the alpine study area. However, this reduction was likely to have a small impact on the population growth rate. Hence, we concluded from this that reduction in food supply is not sufficient to generate demographic feedbacks that will result in a stationary distribution (fluctuations around some mean density with a bounded variance)

of population densities, which is a necessary condition for population regulation (Turchin 1995).

This extrapolation from the individual up to the population level assumes the existence of an inverse relationship between population density and per capita availability of winter food for moose. This assumption is likely to be fulfilled in the moose because, at the individual level, daily resource consumption decreases (Andersen and Sæther 1992) and the proportion of the food supply that is removed increases with decreasing food availability (Sæther and Andersen 1990). Furthermore, a decrease in the resource supply with increasing population density has been documented in other large ungulates such as the reindeer (Leader-Williams 1988, Skogland 1990), and is likely to occur in moose as well.

Crête strongly argued that our results would have been more easily interpretable if we had been able to present data on the size of our populations in relation to the carrying capacity (K; i.e., the density at which the population growth rate is 1). However, reliable estimates of K are extremely difficult to obtain for long-lived and hunted species such as the moose, for two main reasons: (1) In such a variable environment as inhabited by moose in our Norwegian populations, stochastic variation in climate is likely to generate considerable annual variation in K (Sæther 1985). (2) The age distribution of many hunted moose populations is unstable, which may generate large annual variation in recruitment. In addition, there is large, natural, regional variation within Fennoscandia in the quantity and quality of available food for moose, probably related to differences in climate and topography. Thus, it is impossible to make inferences about K as done by Crête just by comparing the range of variation in densities across populations.

Although K will be extremely difficult to estimate in long-lived species such as the moose, we suggest that the population size in our alpine study area (the population with the lowest per capita intake rate) was close to K (or even larger) during the study period. During the winters of 1980–1983, the mean number of moose censused in this study area with a combination of fixed-wing aircraft and track counts was 263 animals (Andersen 1991). Assuming 100% detectability, an unrealisticly high figure for such censuses (Gasaway et al. 1986), this implies a minimum density of 7.4 moose/km² of forested area. Considering the low resource availability in the area due to a very long period with high moose densities, we suggest that this represents such an extreme density of moose that first-year mortality, in particular, should be expected to be high if any regulatory effects exist. Aerial censuses were also conducted in the northern study area (B. E. Sæther, E. J. Solberg, and M. Heim, *unpublished data*). Using a helicopter and correcting for census biases (90%, B. E. Sæther, E. J. Solberg, and M. Heim, *unpublished data*), 2.1 animals were recorded per square kilometer of forested area during the winter of 1997, which is less than one third that in the alpine area. However, the highest mortality rate was recorded in the northern study area (Sæther et al. 1996).

We conclude that the data from our alpine study area are likely to represent a situation that occurs at very high population densities. In spite of the large variation in winter population density between two of the study areas, only small demographic differences were recorded. Thus, the arguments advanced by Crête that we should consider the effects of population density have not altered any of our conclusions. In fact, we consider the objections raised by Crête to illustrate a common misconception that population phenomena can only be studied at the population level. As argued elsewhere (Sæther 1997), we think that long-term studies of individual variation in reproduction and survival are often necessary for an understanding of the mechanisms generating variation in population size of long-lived species such as large ungulates.

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