

# The Magnitude of Local Host Specificity for Phytophagous Insects and its Implications for Estimates of Global Species Richness

FRODE ØDEGAARD,\*‡ OLA H. DISERUD,† STEINAR ENGEN,†  
AND KAARE AAGAARD\*

\*Norwegian Institute for Nature Research, Tungasletta 2, N-7485 Trondheim, Norway

†Norwegian University of Science and Technology, Department of Mathematical Sciences, N-7491 Trondheim, Norway

---

**Abstract:** *Estimates of the global number of arthropod species range from 2 million to more than 30 million species. One of the most critical assumptions affecting the higher of these estimates is the assumed magnitude of host specificity of phytophagous insects, which varies considerably. Difficulties in estimating this value are caused by both lack of satisfactory data sets and lack of methods for its objective calculation. We provide a new method for predicting host specificity for phytophagous insects at a local scale based on the concept of effective specialization. When the insect-plant host associations of a restricted number of plant species are known, we can predict the magnitude of host specificity when more plant species are included. Based on 2561 host observations of 697 beetle species on 50 plant species in the canopies of a tropical dry forest in Panama, we predict that host specificity for adult phytophagous beetles in this forest range from 7% to 10%. These values suggest that the higher estimates of global species richness are not tenable.*

Magnitud de la Especificidad de la Relación Insecto Fitófago-Planta Hospedero y sus Implicaciones para la Estimación de la Riqueza Específica Global

**Resumen:** *Las estimaciones del número global de artrópodos varían entre 2 y más de 30 millones de especies. Uno de los supuestos críticos que afectan las estimaciones más altas es la presunta alta especificidad en la interacción insecto fitófago-planta hospedero. Estas estimaciones son sumamente variables debido a las dificultades para estimar correctamente el grado de especificidad, tanto por la escasez de datos empíricos satisfactorios, como por la falta de una metodología que permita una estimación objetiva de la interacción. En el presente trabajo proponemos un método nuevo para predecir la especificidad de la interacción fitófago-planta hospedero a una escala local, basado en el concepto de la "especialización efectiva." Cuando se conocen las asociaciones insecto-planta hospedero para un número restringido de plantas, se puede predecir el grado de especificidad de la interacción para un número mayor de especies vegetales. En base a 2561 observaciones de 697 especies de coleópteros en 50 especies vegetales del dosel de un bosque tropical seco de Panamá, predecimos que la especificidad de los coleópteros fitófagos adultos con sus plantas hospedero es de un 7-10%. Estos valores no corroboran los valores más altos de las estimaciones actuales de la riqueza específica a nivel global.*

---

‡email frode.odegaard@ninatrd.ninaniku.no

Paper submitted August 23, 1999; revised manuscript accepted January 12, 2000.

## Introduction

Phytophagous insect species show a sliding degree of host specificity from strictly monophagous to broadly polyphagous. Calculation of the magnitude of host specificity, therefore, must give every insect species an inverse weight in accordance with the number of hosts on which the insect species is found (May 1990; Mawdsley & Stork 1997). Consequently, the monophagous species are the most important component of the parameter, and the importance of the other insect species decreases with their increasing degree of polyphagy. This concept, termed effective specialization, was introduced by May (1990) for the calculation of the host specificity of phytophagous insects in a local community.

Effective specialization  $F_T$ —equivalent to the parameter  $f$  in May (1990) and  $x$  in Thomas (1990)—of insect species associated with a set of plant species in a community may be expressed as

$$F_T = S_T / (\bar{S}_T \times T), \quad (1)$$

where  $T$  is the number of plant species,  $S_T$  is the total number of different insect species associated with  $T$  plant species, and  $\bar{S}_T$  is the average number of insect species associated with each plant species (May 1990; Mawdsley & Stork 1997). Therefore,  $\bar{S}_T \times T$  is the number of host observations. Accordingly, effective specialization is simply the pooled number of plant-associated insect species divided by the number of host observations of those insects.

In a community defined by  $T$  plant species,  $F_T$  is given by equation 1 if all host associations of all plant species are known. The magnitude of  $F_T$  depends on  $T$ , however. A data set obtained from only one plant species gives an  $F_T$  of 1 (100% host specificity) because  $S_T = \bar{S}_T \times T$ . In a data set obtained from two plant species,  $F_T$  will decrease if some of the insects share the two host plants. Finally, an inverse relation between  $F_T$  and  $T$  will appear when more plant species are included.

Effective specialization is directly relevant to studies of local species richness, community structure, and various aspects of insect-plant interactions (Mawdsley & Stork 1997). It is also utilized in estimates of global insect species richness either directly (Erwin 1982) or indirectly through the use of a between-community correction factor (Thomas 1990) that is required because of the considerable variation of the phenomenon across spatial scales (Fox & Morrow 1981; May 1990; Radtkey & Singer 1995). In global estimates of insect species richness, the magnitude of effective specialization of insects associated with tropical trees is estimated variously from 3% up to 20% (Erwin 1982; Stork 1988; May 1990; Basset 1992). The magnitude of local host specificity is known only for particular ecological situations at restricted taxonomic scales and undefined spatial scales (Futuyma & Gould 1979; Thomas 1990). Therefore,

there is great need for comparable data sets to produce objective measurements of local host specificity. An examination of the relationship between  $F_T$  and  $T$  elucidates fundamental aspects of this phenomenon. Our study aims to outline two of these, (1) the magnitude of local host specificity for insects in a plant community and (2) possible differences in local host specificity among different growth forms of plants.

## Methods

We elucidate these relationships using an empirical data set based on a study of adult phytophagous beetles (Buprestidae, Chrysomeloidea, and Curculionoidea) associated with 24 tree species (2 replicates of 13 species) and 26 liana species (2 replicates of 14 species). From a tower crane, beetles were collected by hand from the canopy of a tropical dry forest (0.8 ha) in Parque Natural Metropolitano, Panama Province, Panama (Ødegaard 2000). Host associations were revealed by feeding behavior and probability-based host observations, according to Flowers and Janzen (1997). This sampling procedure ensured that insect species accidentally occurring on a plant would be omitted. The plants were not completely sampled. If the proportion of monophagous species is maintained after additional host observations, however, then additional sampling would not significantly affect the magnitude of effective specialization (Diserud & Ødegaard 2000).

From our data set,  $F_T$  can be calculated as a function of  $T$ . We let  $T$  range from 1 to the total number of plant species in our sample (50), and we let  $F_T$  be the average over all possible combinations of  $T$  plant species from our sample (Krylov 1971). This nonparametric subsampling technique gives the magnitude of effective specialization for subsamples of 1, 2 . . . 50 plant species in our data set. To extrapolate, we needed a parametric model that would allow us to predict effective specialization when we expanded the community to include more plant species. Theoretically, each insect species was assigned a probability ( $p$ ) corresponding to the proportion of the host species in the community this insect species was expected to be utilizing. Following Engen and Lande (1996a, 1996b), whose results were generated based on a stochastic evolutionary process, we assumed that the insect species' probabilities,  $p$ , were realizations of an inhomogeneous Poisson process. The model is therefore, at a given point of time and space, completely defined by the rate  $\lambda(p)$  of this process. This rate was assumed to be proportional to the beta distribution,

$$\lambda(p) = c p^{k-1} (1-p)^{\beta-1} \quad (2)$$

where  $k > -1$ ,  $\beta > 0$ , and  $c$  is a proportionality constant. We then propose a binomial sampling procedure,

so that when the number of different host species  $T$  in the sample is known, the number of host observations for an insect species will be binomially distributed ( $T, p$ ; Diserud & Ødegaard 2000).

For a given data set, we can now estimate the parameters in our model by maximum likelihood estimation theory. The extrapolation of  $F_T$  beyond the number of host species in the data set demands that we substitute  $S_T$  and  $\bar{S}_T$  in equation 1 with their expectations,  $E(S_T)$  and  $E(\bar{S}_T)$ , respectively,

$$F_T = E(S_T)/E(\bar{S}_T) \times T. \quad (3)$$

## Results and Discussion

One year of study produced 35,479 individuals belonging to 1,167 species of phytophagous beetles, of which 697 species gave a total of 2,561 host associations (Ødegaard 2000).

A comparison of our parametric model with the curve obtained from the nonparametric subsampling technique shows almost identical values of  $F_T$  (Fig. 1), indicating a good fit of the model. In our particular situation, however, there were limits to the extent to which the curve could be extrapolated because the sampling was

performed on plant species at a small spatial scale. The parametric model assumes a sample obtained by random selection of plants from the species list of an area. The sampled area therefore needs to be representative of the extrapolated area. If, for instance, habitat barriers or other vegetation types are encountered, our parameters are expected to change (Diserud & Ødegaard 2000). An extrapolation up to 300–550 plant species (trees >10 cm diameter at breast height and lianas) in this type of forest probably would not be problematic if species numbers of plants in this area were assumed to be similar to those of Costa Rican dry forests (Janzen & Liesner 1980). Furthermore, abundant plant species are probably overrepresented in the sample because of their higher encounter frequency at smaller spatial scales. This fact can bias the data if the host specificity of insects associated with rare and common trees is different. Data given by Southwood (1960), however, suggest that this effect is not significant.

When excluding epiphytes, which are insignificant in tropical dry forests (Gentry & Dodson 1987), we predict that host specificity will approach 10% in the canopies of a forest consisting of 300 plant species and 7% in a forest holding 550 plant species (Fig. 2a). If we include other life forms of plants (e.g., herbs and shrubs), the development of  $F_T$  depends on the extent of the fauna

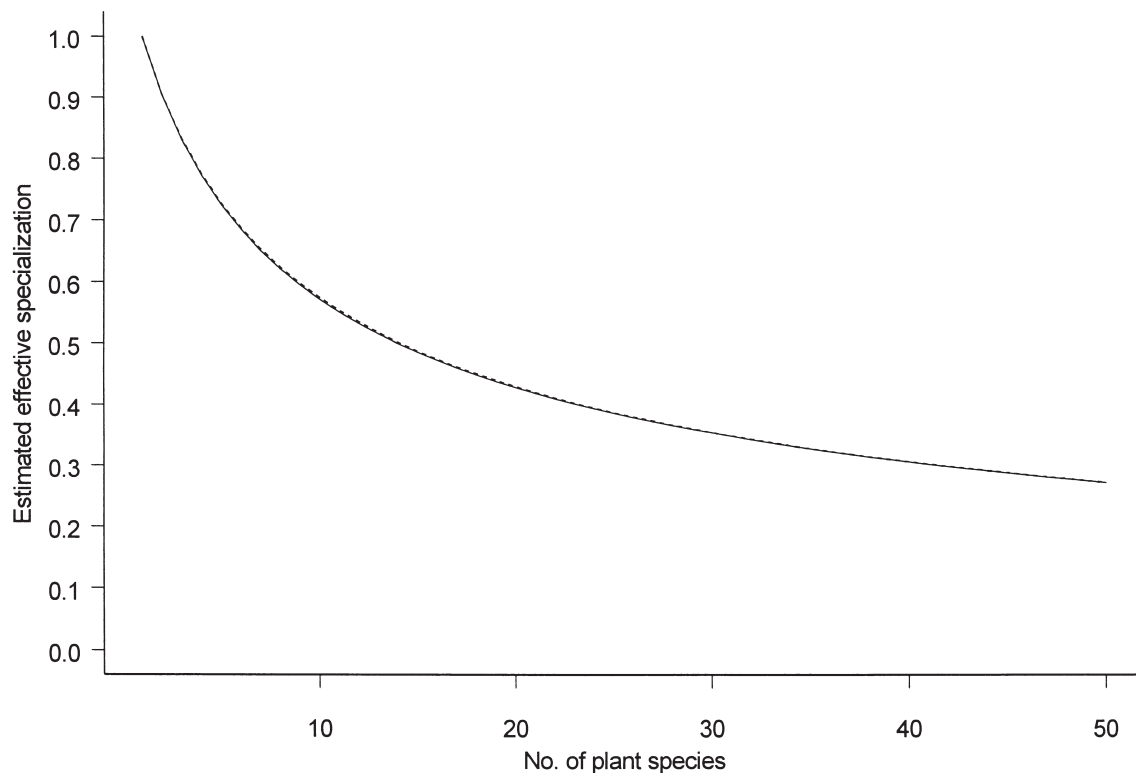
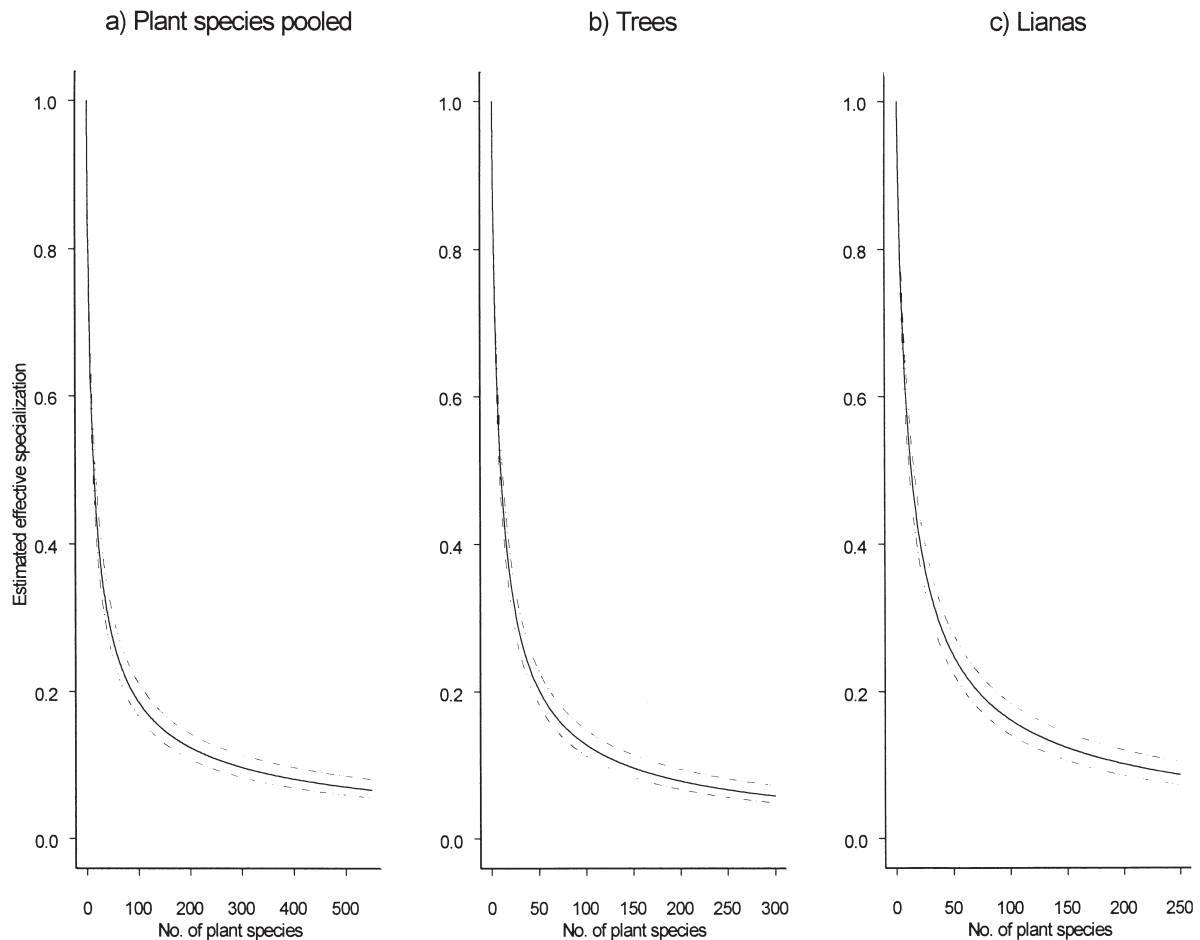


Figure 1. Estimated effective specialization as a function of the number of plant species ( $T$ ). The nonparametric curve (solid line) and the beta binomial model (dotted line) are compared and are nearly indistinguishable. The parameters of the model ( $k, \beta$ ) were estimated as  $-0.29$  and  $3.0$ , respectively.



**Figure 2.** Estimated effective specialization as a function of the number of plant species according to the beta binomial model and with approximate 95% confidence belts indicated by the dotted lines: (a) if the number of plant species in Neotropical dry forests ranges from 300 to 550 species of trees (>10 cm diameter at breast height) and lianas, depending on area, then host specificity is predicted to range from 10% to 7%; (b) if tree species are treated separately, host specificity for phytophagous beetles in a tropical dry forest of 150–300 tree species ranges from 10% to 6%; and (c) similarly, host specificity for phytophagous beetles in a tropical dry forest of 150–250 liana species would range from 12% to 9%. Parametric bootstrapping yields an uncertainty of 1.3% for the estimated value of effective specialization when the growth forms of plants are pooled ( $T = 550$ ). For trees ( $T = 300$ ) and lianas ( $T = 250$ ) separately, the uncertainty for the estimated value of effective specialization is 1.3% and 1.8%, respectively.

shared between life forms. If only trees are considered, host specificity would range from 10% to 6% when  $T$  ranges from 150–300 species, respectively (Fig. 2b). This result corresponds well with indirect analysis of effective specialization of the beetle fauna associated with four species (10 individuals) of Bornean trees (Mawdsley & Stork 1997), which indicates an average effective specialization of <5% (Stork 1997). Similarly, a study of host specificity based on feeding trials of insects associated with 10 tree species in Papua New Guinea indicated that 4.3% of the unpooled insect species were likely to be monophagous in that system (Basset et al. 1996a). The host specificity of liana-associated beetles has never been elucidated. We predict that host specificity would range from 12% to 9% for beetles associated

with 150–250 liana species, respectively (Fig. 2c), indicating that liana associates are more specialized than those on trees. Generally, parametric bootstrapping, at a 95% confidence level, enabled us to predict the host specificity with an uncertainty of 1.3% for plant species pooled ( $T = 550$ ) and for trees separately ( $T = 300$ ). For lianas, the uncertainty of the estimated host specificity was 1.8% ( $T = 250$ ).

## Conclusion

The higher estimates of 30 million or more arthropod species on Earth are extrapolated from samples and are based on Erwin's assessment of 20% host specificity

(Erwin 1982; May 1988; Stork 1988; Gaston 1991; Hodkinson & Casson 1991; Gaston 1992; Stork 1993). Assuming that beetles make up 20% rather than 40% of tropical arthropod species (Thomas 1990) and setting aside other controversies in these estimates (Stork 1988; May 1990; Thomas 1990; Gaston 1991; Hodkinson & Casson 1991; Hammond 1992; Basset et al. 1996b; Mawdsley & Stork 1997), one can recalculate these estimates based on our predicted magnitude of host specificity. The results from these recalculations fit well within the interval of 5–15 million species, a number indicated from most other independent estimation methods for global species richness (Stork 1993).

## Acknowledgments

We thank the Smithsonian Tropical Research Institute for providing access to the crane, T. L. Erwin, O. T. Sandlund, B. Å. Tømmerås, Å. Viken, and S. J. Wright for discussions and critical comments on the manuscript. The study was funded by grants from the Norwegian Research Council and the Norwegian Institute for Nature Research.

## Literature Cited

- Basset, Y. 1992. Host specificity of arboreal and free-living insect herbivores in rain forests. *Biological Journal of the Linnean Society* **47**: 115–133.
- Basset, Y., G. A. Samuelson, A. Allison, and S. E. Miller. 1996a. How many species of host-specific insects feed on a species of tropical tree. *Biological Journal of the Linnean Society* **59**:201–216.
- Basset, Y., G. A. Samuelson, and S. E. Miller. 1996b. Similarities and contrasts in the local insect faunas associated with ten forest tree species of New Guinea. *Pacific Science* **50**:157–183.
- Diserud, O. H., and F. Ødegaard. 2000. The beta binomial model for host specificity among organisms in trophic interactions. *Biometrics* **56**:16–22.
- Engen, S., and R. Lande. 1996a. Population dynamic models generating lognormal species abundance distribution. *Mathematical Bioscience* **132**:169–183.
- Engen, S., and R. Lande. 1996b. Population dynamic models generating species abundance distributions of the gamma type. *Journal of Theoretical Biology* **178**:325–331.
- Erwin, T. L. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin* **36**:74–75.
- Flowers, R. W., and D. H. Janzen. 1997. Feeding records of Costa Rican leaf beetles (Coleoptera: Chrysomelidae). *Florida Entomologist* **80**: 334–366.
- Fox, L. R., and P. A. Morrow. 1981. Specialization: species property or local phenomenon? *Science* **211**:887–893.
- Futuyma, D. J., and F. Gould. 1979. Associations of plants and insects in a deciduous forest. *Ecological Monographs* **49**:33–50.
- Gaston, K. J. 1991. The magnitude of global insect species richness. *Conservation Biology* **5**:283–296.
- Gaston, K. J. 1992. Regional numbers of insect and plant species. *Functional Ecology* **6**:243–247.
- Gentry, A. H., and C. Dodson. 1987. Contribution of nontrees to species richness of a tropical rain forest. *Biotropica* **19**:149–156.
- Hammond, P. M. 1992. Species inventory. Pages 17–39 in B. Groombridge, editor. *Global biodiversity: status of the Earth's living resources*. Chapman and Hall, London.
- Hodkinson, I. D., and D. Casson. 1991. A lesser prediction for bugs: Hemiptera (Insecta) diversity in tropical rain forests. *Biological Journal of the Linnean Society* **43**:101–109.
- Janzen, D. H., and R. Liesner. 1980. Annotated check-list of plants of lowland Guanacaste province, Costa Rica, exclusive of grasses and non-vascular cryptogams. *Brenesia* **18**:15–90.
- Krylov, V. V. 1971. On the station-species curve. Pages 233–235 in G. P. Patil, E. C. Pielou, and W. E. Waters, editors. *Statistical ecology 3. Many species populations, ecosystems and system analysis*. Pennsylvania State University Press, Pennsylvania.
- Mawdsley, N. A., and N. E. Stork. 1997. Host-specificity and effective specialization of tropical canopy beetles. Pages 104–130 in N. E. Stork, J. Adis, and R. K. Didham, editors. *Canopy arthropods*. Chapman & Hall, London.
- May, R. M. 1988. How many species are there on earth? *Science* **241**: 1441–1449.
- May, R. M. 1990. How many species? *Philosophical Transactions of the Royal Society of London B* **330**:293–304.
- Ødegaard, F. 2000. The relative importance of trees versus lianas as hosts for phytophagous beetles (Coleoptera) in tropical forests. *Journal of Biogeography* **27**:in press.
- Radtkey, R. R., and M. C. Singer. 1995. Repeated reversals of host-preference evolution in a specialist insect herbivore. *Evolution* **49**:351–359.
- Southwood, T. R. E. 1960. The abundance of the Hawaiian trees and the number of their associated insect species. *Proceedings of the Hawaiian Entomological Society* **17**:299–303.
- Stork, N. E. 1988. Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society* **35**:321–337.
- Stork, N. E. 1993. How many insect species are there? *Biodiversity and Conservation* **2**:215–232.
- Stork, N. E. 1997. Measuring global biodiversity and its decline. Pages 41–68 in M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson, editors. *Biodiversity II*. Joseph Henry Press, Washington, D.C.
- Thomas, C. D. 1990. Fewer species. *Nature* **347**:237.

